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**SILK USE DURING MATING IN
PISAURINA MIRA (WALCKENAER)
(ARANEAE, PISAURIDAE)**

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ABSTRACT

The mating behavior of the nursery web spider *Pisaurina mira* is described for the first time. These spiders mate while suspended from draglines as in *Oxyopes heterophthalmus* (Latr.) and *Peucetia viridans* (Hentz). The unique feature of the mating in *P. mira*, however, is the male's use of a veil of silk to wrap the female's legs I and II into a flexed position prior to copulation while her legs III and IV are held in a flexed position by the male's embrace. Mating is accomplished in a version of position II with body axes in a right angle as the female is cradled by the male's legs. The use of silk to "tie" the female is reported elsewhere only in *Xysticus*.

INTRODUCTION

Pisaurina mira (Walckenaer) is known to use silk in the construction of the nursery, egg sac, and juvenile web (Carico 1972, 1985). The purpose of this paper is to describe for the first time the mating sequence of *P. mira* which includes the unique use of silk to bind the female's legs I and II during copulation.

MATERIALS AND METHODS

Observations were made in the laboratory on spiders that were collected at night in Lynchburg, Virginia, and in Fairhaven, New Jersey, during the months of May and June during 1984-85. One field observation of mating revealed no differences from those observed in the laboratory. Male and immature female spiders were kept in glass jars and plastic containers between mating bouts. Mature females were kept in separate aquaria, and some matings were observed in these containers. All spiders were fed blowflies (*Sarcophaga* sp.) and houseflies (*Musca domestica*) on alternate days.

To observe and record the mating sequence in the laboratory, a non-enclosed mating arena was devised using potted philodendron (*Philodendron scadens oxycardium*) or English ivy (*Hedra helix*) set in large, shallow trays of water. The water discouraged escape, and thus made possible an unobstructed view of behavior. Events were recorded with color video cameras and 35 mm cameras.

¹Send correspondence to JEC.

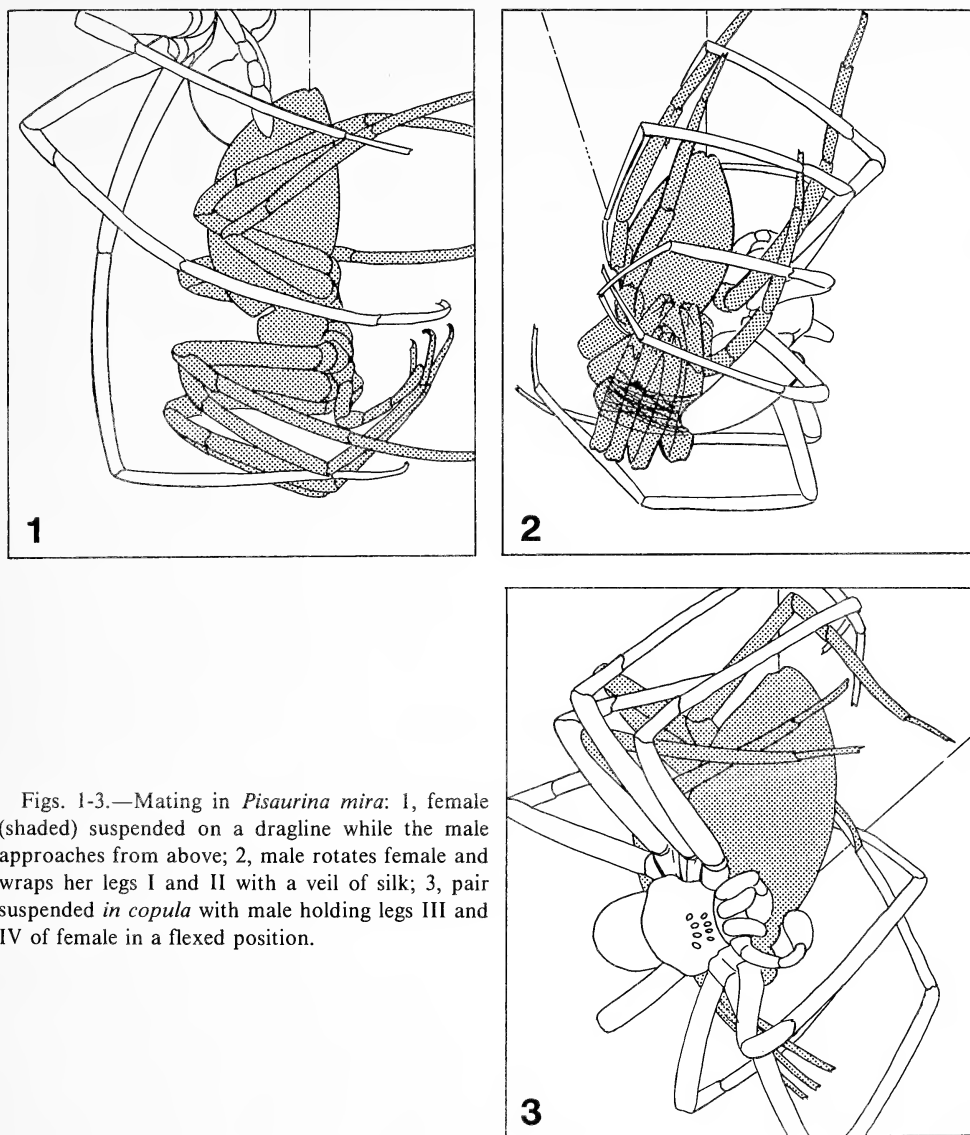
RESULTS

Communication before mating.—In a typical observational session, the female was first introduced onto the plant, upon which she subsequently laid down a series of draglines, by moving upward and across the outer parts of the plant. The male was introduced onto the plant 15 minutes to 3 hours after her wandering activity subsided. He wandered randomly across the plant, climbing and descending until he contacted her dragline. He then followed the dragline, passing the prolateral surface of each palpus alternately over it in a lycosid-like manner, similar to that reported for *Lycosa rabida* Walckenaer (Tietjen and Rovner 1980). During the process of his trail-following behavior, the male periodically stopped, released the dragline, and raised and extended either leg I. The time duration of each pause (30 sec-5 min) increased inversely with the distance to the female (20.3 cm-2.5 cm). There was no visible response by the female. Gradually, the distance between members of the mating pair decreased until the male touched her hind legs with his legs I and II, resulting in leg interplay between the sexes. In each instance, the tarsal portion of the male's leg made contact with her tibiae, metatarsi and sometimes patellae.

Mating.—When she was not receptive, the female climbed a short distance and descended immediately on a line to the lower branches of the plant. When she was receptive, the pair remained in contact while in a stationary position for a period of 5-20 sec. She then climbed the remaining distance to the mating area (a leaf or stem) where she attached a dragline and moved to a position beneath. Without pause, he approached from her posterior and moved to a location directly above her. He moved laterally across the edge of his perch as she drew her legs I and II against her carapace and descended freely (1.6-3.8 cm) on her dragline. She was thus suspended free in space, face downward, inactive (possibly in a cataleptic state) and tethered only by a dragline (Fig. 1). He descended after her on his dragline, while following her dragline with his leg I. He moved across the dorsal surface of her abdomen, using his legs I and II and palps to rotate her as he moved to her ventral surface. As he rotated her three to five times, he pulled a veil of silk across her legs and bound them in a flexed position (Fig. 2). After he completed the veil, he attached his dragline to her legs I and II, which left her suspended on two draglines.

To prepare for copulation he cradled her body with his legs, "folded" her legs III and IV into a flexed position, and assumed a version of position II with body axes at right angles (Fig. 3). While in this position he paused to pass his palps through his chelicerae to moisten them before insertion. The left palpus was then applied to the left atrium of her epigynum, and, after shifting his body to the other side, the right palpus was applied to the right atrium. The palpal bulb remained expanded 20-30 sec during each insertion of the embolus. There was a total of three to five insertions with a shift of the body between each insertion.

The female became increasingly active during the final insertion, which indicated that the state of receptivity had ended. He discontinued cradling her with his legs, and her legs III and IV assumed an extended position. He wrapped her legs I and II with an additional veil of silk, climbed over her ventral surface and onto her dragline, leaving her bound and suspended on the line. He retreated to the lower portion of the plant while she freed herself from the silken veil and descended on her line to another location on the plant.



Figs. 1-3.—Mating in *Pisaurina mira*: 1, female (shaded) suspended on a dragline while the male approaches from above; 2, male rotates female and wraps her legs I and II with a veil of silk; 3, pair suspended in copula with male holding legs III and IV of female in a flexed position.

DISCUSSION

Because of the prevailing tendency towards agonistic behavior among spiders—even conspecifics—it seems likely that binding of the female's legs with silk prior to copulation, an apparent advantage for the survival of the male, would be a widespread phenomenon among spiders. To our knowledge, however, wrapping of the female with silk prior to copulation has been described previously only for *Xysticus* (Bristowe 1958). (However, female wrapping by the male has been recently discovered in a Neotropical pisaurid, *Ancylometes bogotensis*; Merrett 1988). In *Xysticus*, the male spins a "bridal veil" of silk across the legs and body of the female to bind her to the substratum, but in *P. mira*, binding of the female occurs in a wrapping fashion while she is suspended free from a dragline. The known differences in detail of the behaviors, along with the well-known

morphological differences between these two spiders, suggest that silk binding of the female was probably derived separately.

The aspect of mating while suspended in space on a dragline is known in some species of Oxyopidae. The descriptions of mating in *Oxyopes heterophthalmus* (Latreille) (Gerhardt 1933) and *Peucetia viridans* (Hentz) (Whitcomb and Eason 1965) agree with our observation of *P. mira* (but with the absence of silk wrapping). In particular, *P. mira* shows the rotation, or "twirling" of the female that is described for *P. viridans*. This agreement may help support the conclusion by Brady (1964) on morphological grounds that there may be a close phylogenetic relationship between the Oxyopidae and Pisauridae.

The wrapping of the female's legs causes, at most, a brief restraint of the female as she becomes active following mating. As a result of subsequent repeated attempts at mating by the male, the additional silk causes the female to be further immobilized. The functional outcome of this wrapping procedure may serve to reduce predation on the male. Because the female's legs are free from any substrate during mating, contrary to the case in most mating spiders, it seems probable that the male's body would be the first object that the female would contact, and therefore, would immediately place him in jeopardy. Having the female's legs restrained, even for a short time, provides what may be the critical opportunity for the male to escape predation by his mate.

Published work on mating behavior in other pisaurids is known to us only for the genera *Dolomedes* and *Pisaura*, and the features of suspension and wrapping of the female are not included in any of these. We suggest that the mating behavior in representative species of other pisaurid genera be investigated for this character along with other characters which could aid in a better understanding of the systematics of this complex family.

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ECOLOGIA Y ASPECTOS DEL COMPORTAMIENTO EN *LINOTHELE* SP. (ARANEAE, DIPLURIDAE)

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ABSTRACT

A species of *Linothele* (Dipluridae), was studied in Soberanía Park (Panamá) and the lower elevation, more humid Department of Chocó (Colombia). The purpose of the study was to determine behavior related to web construction, prey capture, design and trophic efficiency of the web, food source, migration, agonistic behavior and associated kleptoparasites. Differences between temperatures during the day were also studied inside and outside the spider's retreat.

Positive correlations in the variables of body weight vs. body length; weight vs. diameter of the web orifice; body weight vs. the maximum web dimension; body length vs. maximum web diameter were found in both zones.

The webs of these spiders are characterized by having a number of associated symbionts, some of them true kleptoparasites. The spiders discriminate in their choice of prey and are most active at night. There was no evidence that they could excavate their own retreat cavities and they showed high levels of inter- and intraspecific agonistic interactions.

RESUMEN

El trabajo se inició en el Parque de la Soberanía de Panamá y se continuó en Colombia (Departamento del Chocó), siendo ésta última área mucho más lluviosa y de menor altitud.

Se trabajó con una especie de *Linothele* (Dipluridae) con el objetivo de estudiar algunos patrones de comportamiento relacionados con su conducta tejedora; manejo de la presa, patrón y eficiencia trófica de la tela, posibles fuentes de alimento, capacidad migratoria, conducta agonística, cleptoparasitismos, ciclos térmicos entre las 0800; 1200; 1600; 2000, de la temperatura ambiental y la del interior de la cueva; además de algunos aspectos ecológicos.

La correlación de variables (peso x largo corporal; peso corporal x el mayor valor de la dimensión de la tela; peso x diámetro del orificio de la tela; largo corporal x diámetro y por mayor valor de la tela), evidenciaron en las dos zonas de estudios, coeficientes positivos. Además, las telas de estas arañas se caracterizaron por presentar un buen número de simbioses asociados, algunos ocasionales y otros verdaderos cleptoparásitos.

Se encontró que discriminaban presas y no dieron evidencia que contruyen sus propias cuevas; su mayor actividad es nocturna y presenta un alto grado de conducta agonística intra e interespecífica.

INTRODUCCION

Actualmente existe en Colombia un gran vacío científico relacionado con las investigaciones en los diversos aspectos biológicos de nuestra aracnofauna, con excepción de los esporádicos trabajos de tipo taxonómico realizados por misiones extranjeras. Ante tal situación, y luego del conocimiento derivado de la

investigación en el Departamento de Antioquia, Paz (1978), se diseñó este trabajo con el fin de obtener información de aspectos biológicos de una especie del género *Linothele* presente en bosques de Panamá y Colombia, tales como: patrones de comportamiento relacionados con la defensa, captura de la presa, interacciones agonísticas, construcción de redes y eficiencia de las mismas, posibles causas de muerte y migración, discriminación de presas, cleptoparásitos y otros simbioses asociados con la tela, ciclos de temperatura en las cuevas, actividad diurna y nocturna y hasta donde fuera posible, aspectos de su biología reproductiva. Las observaciones se harían sin descuidar las del laboratorio.

Interacciones entre cleptoparásitos y huésped en arañas constructoras de telas aéreas han sido descritas por Thornhill (1975), Vollrath (1978-1979b), Turnbull (1964), Rypstra (1981), Opell y Eberhard (1984); la importancia de las vibraciones inducidas a la tela en la comunicación intra e interespecífica en muchos grupos de arañas, ha sido estudiada o revisada por Walcott (1959), Uetz y Stratton (1983), Parry (1965) y Vollrath (1979a). Robinson and Robinson (1980) han estudiado el afecto de la captura de la presa y de la destrucción de telas orbitales en varios grupos de arañas, lo mismo que su conducta durante el acto de captura de la presa, cortejo, apareamiento, y el comportamiento de construcción de telas.

MATERIALES Y METODOS

La investigación se realizó en dos áreas biogeográficas diferentes: en el Parque de la Soberanía de Panamá y en el Departamento del Chocó (Colombia). En Panamá, (Fig. 1), se trabajó a través de la carretera que desde Gamboa conduce al antiguo oleoducto del Darién (Pipeline-Road), cruzando un extenso bosque primario muy bien conservado, con alturas sobre el nivel del mar comprendidas entre los 180 y 250 m, una temperatura promedia de 26.8° C (max = 30°; min = 24.4°) y una humedad relativa promedia anual de \pm 80%. En este bosque primario seco, los nidos de arañas predominan a nivel de borde de quebradas principalmente.

El área de estudio en Colombia (Fig. 2), correspondió a un vasto sector comprendido entre Tutunendo—Quibdó y Yuto, sitios de fácil exploración aún durante horas nocturnas. Allí las condiciones climáticas son mucho más inestables que en el sector de Panamá, con alturas sobre el nivel del mar comprendidas entre los 40 y los 56 m, temperatura promedia diaria con máximas y mínimas similares al área de Panamá y una humedad relativa promedio anual entre 86 y 96%.

En ambas áreas, luego de su respectivo reconocimiento fisiográfico, se seleccionaron los sitios de trabajo en concordancia con la abundancia de nidos y la facilidad de tránsito. Así, se procedió a marcar (con cinta roja) y a medir las dimensiones de las telas visibles. Las medidas se tomaban a partir del orificio de entrada de la cueva, frontalmente hacia el observador (L = largo) y en sentido transversal pasando por el orificio de la tela (A = ancho), además se determinaba el valor del diámetro del orificio de entrada a la cueva.

Si la ubicación de la tela lo permitía, se procedía a tratar de capturar la araña, induciendo su salida con presas de artrópodos vivos o con umbrales de vibraciones artificiales producidas con una varilla delgada o bien cavando con una barra o pala pequeña. Si la araña se capturaba se medía su longitud desde la

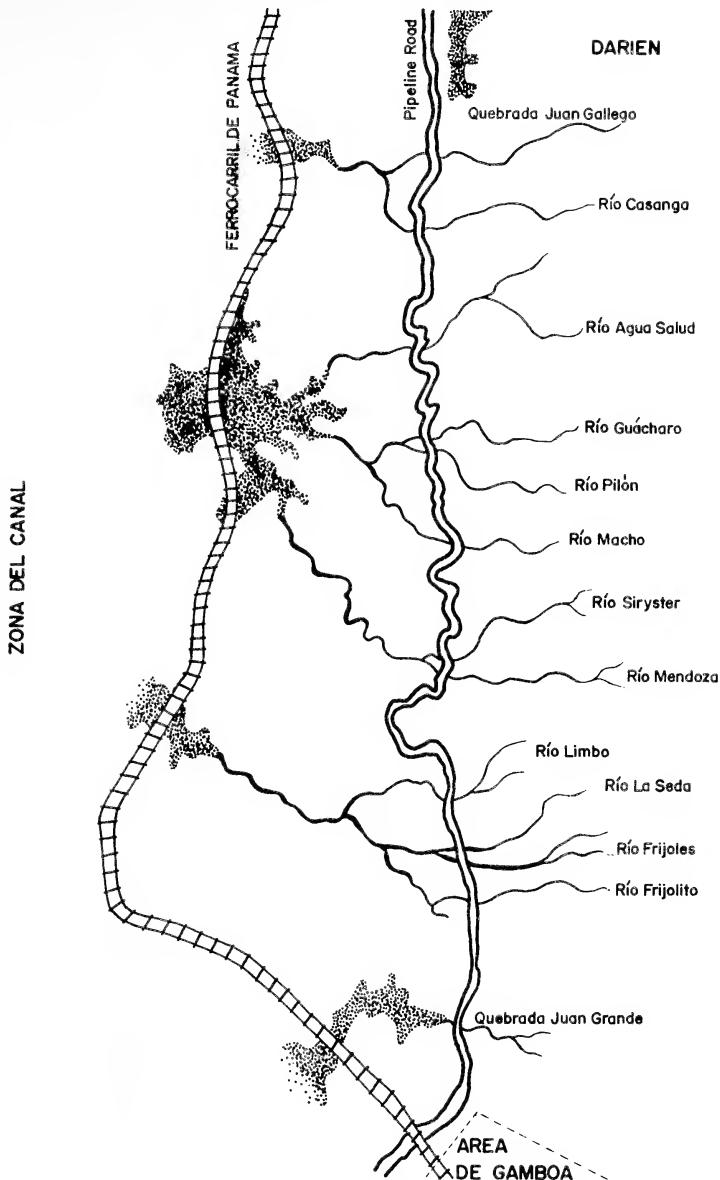


Fig. 1—Croquis del área dentro del “Parque de la soberanía de Panamá”.

inserción de los queliceros hasta el tubérculo anal y luego se le pesaba viva encerrada dentro de un pequeño recipiente plástico con una balanza Ohaus modelo—700. La araña podía traerse al laboratorio para marcar su cefalotórax, con líquido corrector para escritura a máquina o vinilo y regresarla a un sitio distinto o al de captura, bien sobre la tela o en la cueva, para determinar su capacidad de residencia en el lugar (o de migración en caso de encontrarla posteriormente en nuevas telas o sitios). Al cavar los nidos se procuró seguir el patrón arquitectónico del tunel para apreciar su complejidad (Figs. 3 a 6).

Algunas arañas marcadas se trasladaron de un lugar a otro, donde se soltaban o se colocaban en depresiones naturales o hechas por nosotros con el fin de

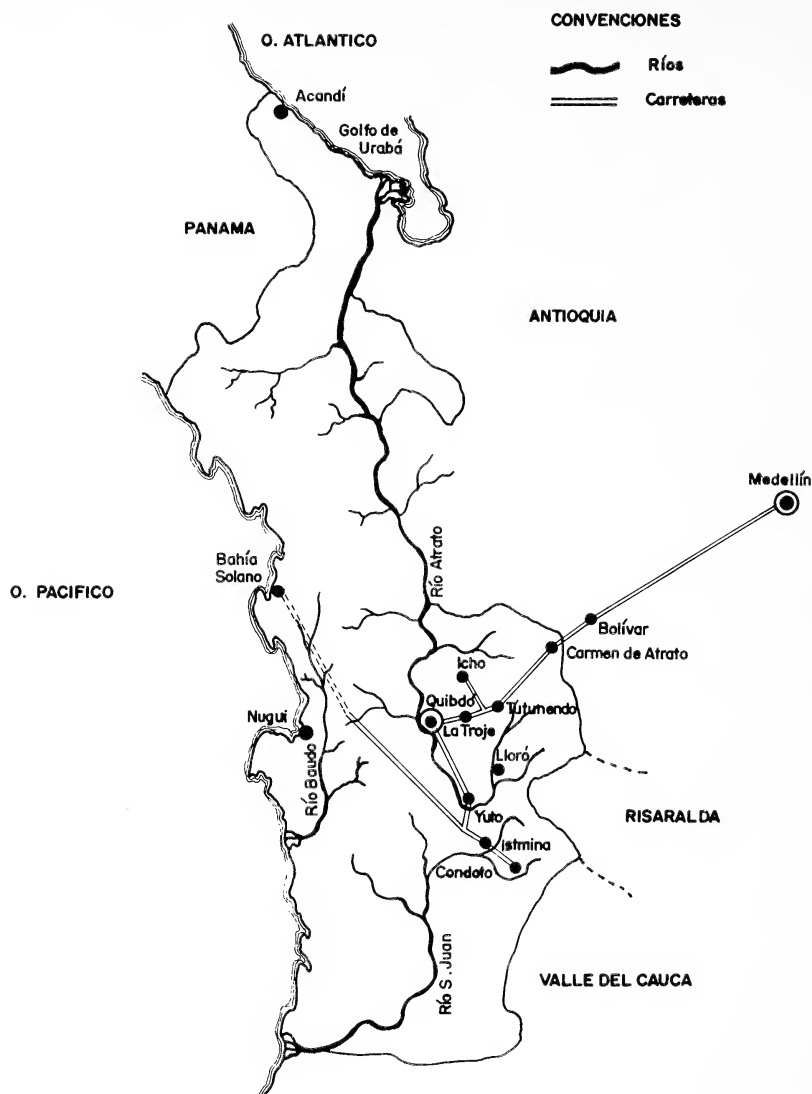


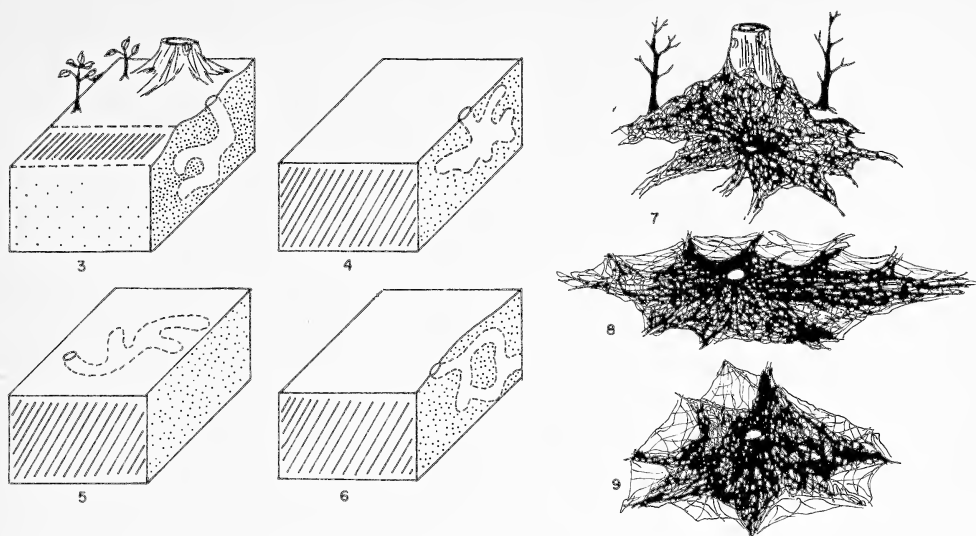
Fig. 2.—Croquis del área del Chocó.

determinar si las mismas cavaban su propia cueva tejiendo luego la tela; o si aprovechaban las depresiones naturales existentes. Lo anterior, porque durante las excavaciones se encontraron pequeños montículos de tierra removida al parecer por la araña.

Su mantenimiento en condiciones de cautiverio se llevó a cabo en nuestra microestación biológica en recipientes de plásticos, en donde recibían el ciclo normal de luz y oscuridad.

Con intervalos de cuatro horas, se determinó la existencia de diferencias de temperatura en el ambiente de las cuevas y de su medio circundante, procediéndose para ello a medirla con un termómetro electrónico Cole/Parmer/Chicago a las 0800; las 1200; las 1600 y las 2000.

La posible actividad de los cleptoparásitos y otros simbioses asociados, se trató de determinar principalmente en las telas de bosque por su relativa abundancia en relación con las telas de las áreas de borde de carretera.



Figs. 3-9.—Diagramas correspondientes a algunos de los perfiles subterráneos de las cuevas y patrones de telas observadas para nidos de *Dipluridae*: 3-6, patrones de cuevas encontrados en terrenos arcillosos; 7-9, patrones de telas con su orificio central.

Las observaciones de interacciones agonísticas intra e interespecíficas se hicieron capturando ejemplares de *Linothele* u otros géneros y se marcaba la araña considerada intrusa.

Para la identificación de los ejemplares de ambas áreas y de los simbiontes asociados a las telas, se enviaron muestras a especialistas como los doctores R. J. Raven; H. W. Levi; B. D. Opell y otros se identificaron con material bibliográfico tales como: Kaston (1978); Forster y Platnick (1977); Exline (1962); Petrunkevitch (1925, 1929); Levi (1963, 1967) y Gertsch (1979).

RESULTADOS Y DISCUSION

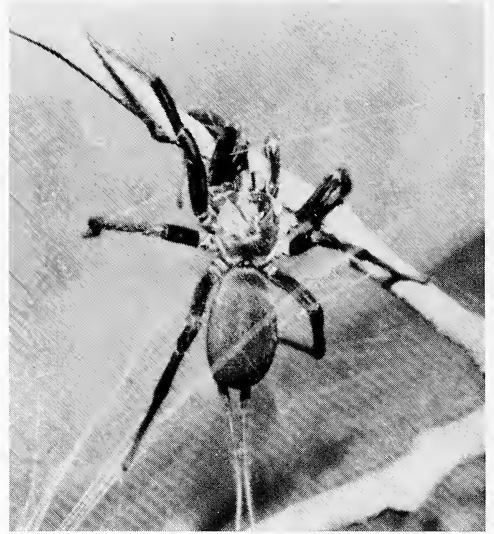
En el área de Panamá, los nidos de estas arañas se comenzaron a encontrar a los 4,000 m, de penetración a partir de Gamboa (sobre el canal), con incremento de abundancia desde río Sirystes hasta el sector de agua—salud. En Colombia, los nidos predominaron sobre los bordes de carreteras, lo que hizo más fácil el trabajo con las telas marcadas. Las arañas fueron identificadas como *Linothele* sp. por R. J. Raven (Queensland Museum, Australia), quien consideró que posiblemente pertenecían a la misma especie, por lo cual trabajaría en su determinación final.

Los ejemplares de Panamá (Fig. 10), se caracterizaron por presentar una coloración café con visos satinados en su cefalotórax, dada por una tupida red de vellosidades sobre su cefalotórax. Abdominalmente las vellosidades son más esparcidas y el matiz cromático que le dan al abdomen es de una coloración más opaca. Su tela es más enmarañada.

Los ejemplares de Colombia, presentan una coloración somática más críptica, con la coloración del cefalotórax más opaco, con visos entre verde, ocre y con una marcada marginación colateral café. Su tela ligeramente menos enmarañada.

Considerando que son de la misma especie, es posible que las diferencias fenéticas entre los dos grupos se deban a factores edáficos y ecológicos y no a que sean especies taxonómicamente diferentes.

Fig. 10.—Hembra de un ejemplar de *Linothele* grávida.



Nido y capacidad territorial.—De nuestras observaciones se puede evidenciar que las arañas de ambas áreas no siguen un patrón secuencial durante la construcción de su complicada tela sobre alguna depresión y tampoco presentan un patrón geométrico fijo detectable en algunas telas de Araneidae las cuales son principalmente aéreas. A pesar de que la construcción y reparación de la tela puede realizarse en cualquier momento, siempre y cuando no existan factores de perturbación, la mayor actividad constructora se realiza durante la noche, período en donde se puede observar a la araña separarse incluso varios metros de la boca del túnel para ubicar los hilos de soporte en extremos opuestos. Durante la reparación o construcción, el desplazamiento de la araña es direccionalmente irregular, hacia adelante, atrás, o a los lados, y con giros abdominales colaterales durante los cuales su par de largas hileras posteriores suelen cambiar de ángulos normalmente con relación al eje hipotético antero-posterior del cuerpo y entre ellas mismas, al acercarse o separarse. Mientras el pequeño par anterior parece producir un tipo de seda que actúa como cemento para pegar entre sí los hilos que conforman la estructura de soporte de la tela y para pegarlos sobre sustratos (hojas, piedras, ramas, tallos, etc.). Los múltiples, transparentes y finos filamentos de seda que emergen de sus hileras posteriores (principalmente del último o tercer segmento), son los responsables de ocasionar el mayor grado de enmarañamiento (Fig. 11).

La tela suele presentar normalmente varios estratos de filamentos de seda a menudo tan bien fusionados que son capaces de retener gotas de agua lo que facilita su visualización durante o después de períodos de lluvia. La boca del túnel queda normalmente en el centro de la asimétrica tela (Figs. 7-9) continuándose con la depresión a través de hilos mediante los cuales la araña, desde el interior de la cueva puede comunicarse con el exterior de la plataforma. La longitud de la depresión suele variar de acuerdo con la naturaleza del terreno y la fisiografía del área, pues las arañas pueden aprovechar grietas externamente pequeñas pero complicadas en el interior, como en ciertos casos de áreas de raíces de árboles o fallas rocosas.

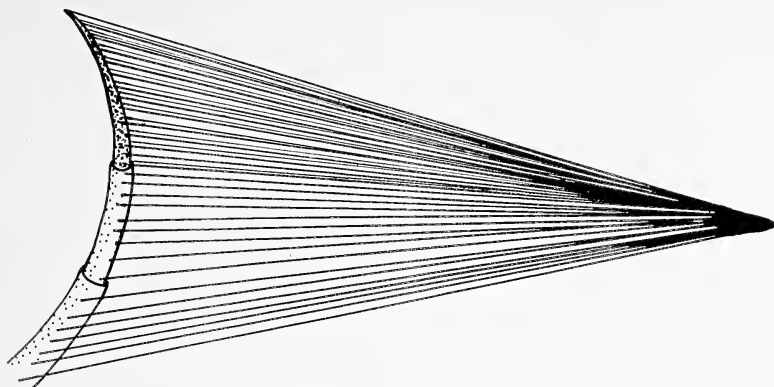


Fig. 11.—Una de las hileras posteriores del abdomen de *Linothele* sp. con filamentos de seda proyectándose desde sus tubuli.

Durante el proceso de construcción o reparación, las arañas suelen acicalarse sus tarsos, metatarsos y en ocasiones desde la patela y tibia cuyos miembros son introducidos doblados y tirados hacia atrás entre los quelíceros.

Cuando se procedía a destruir el nido y su túnel, con el fin de capturar la araña, se observaron ocasionalmente sectores modificados con tierra pulverizada en el piso, lo que nos llevó a pensar que las arañas posiblemente podían intervenir activamente en la fabricación del túnel, de manera especial cuando el terreno era arcilloso y blando. Para corroborarlo se trasladaron 44 ejemplares marcados (incluidas ambas áreas de estudio), de su sitio original a uno nuevo, en donde se les colocaban adyacentes a orificios de depresiones naturales o artificiales (cavadas por nosotros). Revisadas desde el día siguiente durante un mes, se encontró que 13 (29.4%), de estos nuevos sitios fueron abandonados, no así el resto (31 = 70.6%). En ambas situaciones, las arañas no dieron evidencias que pudieran construir sus propios nidos cavando a través de sustrato blando, aunque en 3 ó 4 de los huecos artificiales se encontró algo de tierra pulverizada, cuyo origen no fue posible dilucidarlo. En los 13 nidos abandonados se incluyeron cuatro que no fueron encontrados (perdidos), al parecer por derrumbe. Esta situación además de factores como: área pobre en hojarasca, nido muy expuesto al sol, huecos inundables, pobreza de humedad y predación de roedores u otros, fueron posibles causas del abandono del nuevo sitio. Esta última situación no parece ser muy válida para Colombia, pero sí para Panamá, en donde de acuerdo con M. H. Robinson (comentario personal), él ha observado en la isla de Barro Colorado a los mamíferos *Nasua nasua* (gato solo; cosumbo solo; coatimundi), cavar y alimentarse de tales arañas y de otras como Theraphosidae, que habitan en depresiones subterráneas.

En condiciones de cautiverio, tres de las arañas capturadas se comieron su extensa tela en menos de cinco días y no construyeron nuevamente, lo que evidencia que esta situación también puede presentarse en su ámbito natural aunque se ignoran las causas de esta conducta nidofágica.

Algunas arañas capturadas y colocadas en cautiverio construyeron o iniciaron la construcción de su nido inmediatamente, otras sólo lo hicieron después de varios días o semanas y otras no lo hicieron. Esta conducta parece estar relacionada con estados de gravidez y con el tipo de material presente en el recipiente. Porque en donde se agregaba buena hojarasca con troncos viejos (a los

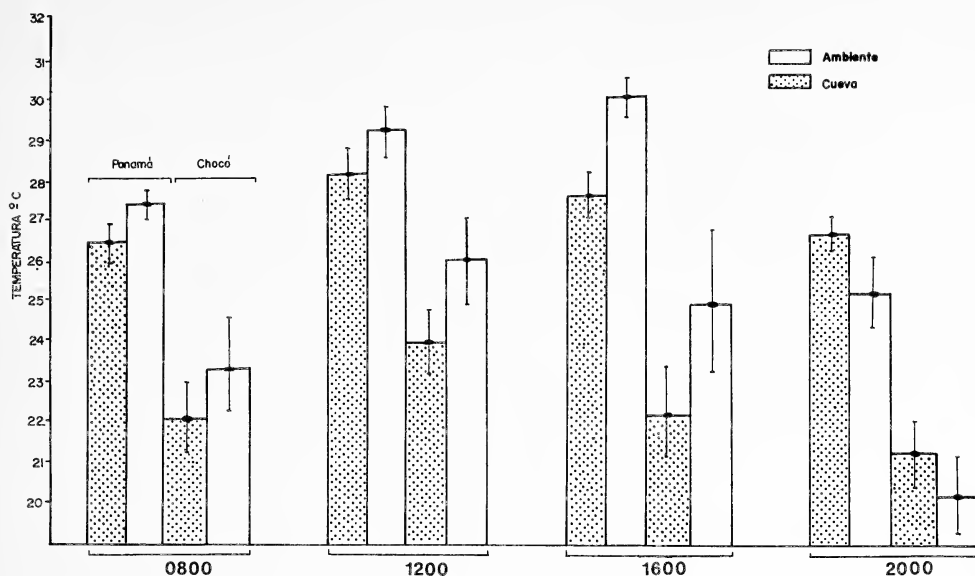


Fig. 12.—Valores de la temperatura promedio (\bar{X}) y su correspondiente d.t. entre las cuevas de telas de arañas y su medio circundante, para las áreas del “Parque de la soberanía de Panamá” y del Chocó, tomadas entre las 0800 y 2000.

que se les había hecho depresiones), ramitas secas y la humedad necesaria, la construcción del nido se inicia más rápidamente.

Algunas arañas capturadas y liberadas de nuevo en sitios diferentes mostraron una conducta muy activa en la búsqueda de depresiones terrestres, pues fuera de su nido parecen ser fácil presa de potenciales predadoras, o pueden morir pronto por acción del calor, como se pudo comprobar aún en los recipientes de colección.

El 80% de las telas marcadas en ambas áreas de estudios permaneció con su araña durante los dos meses del estudio en Panamá y entre los cuatro y seis meses en Colombia.

La tela construida por el macho suele ser mucho más pequeña y en sitios más solitarios.

Ciclos térmicos en las cuevas.—A pesar de que esta variable no evidencia afectar los aspectos del compartamiento estudiado, fue considerada para determinar posibles variaciones térmicas entre el ambiente de las cuevas y su entorno. Tabla 1 y Fig. 12 muestran que los valores promedios para el ambiente de las cuevas fué más baja que la ambiental, excepto para las 2000. Además, que el área de Panamá presenta un mayor grado térmico en relación a la de Colombia, lo que posiblemente se debe a las diferencias en precipitación y por ende de humedad relativa, responsables de que las condiciones climáticas en esta área de Colombia sean más inestables, lo que es reflejado aún en su desviación típica (d.t.). La mayor temperatura de la cueva 2000, en ambas áreas, se debería a la lenta radiación del calor absorbido durante el día por el substrato terrestre.

Relación de variables entre arañas vs tela.—La Tabla 2 muestra los valores mínimos, máximos, promedios y las d.t. del peso y largo corporal de las arañas (P.C. x L.C.); del diámetro del orificio (D.O.) y el mayor valor del tamaño de la tela (M.V.T.) para ambas áreas, en donde los valores son normalmente mayores

Tabla 2.—Representación de los valores mínimos (MIN), máximos (MAX), promedio (\bar{X}) y sus desviaciones típicas (d.t.), de las variables correspondientes al peso y al largo corporal, el diámetro del orificio de la tela y el mayor valor de la tela, tomado entre su largo y su ancho para las dos áreas de estudio.

| Area | P.C. (g) | | | | L.C.(cm) | | | | D.O.(cm) | | | | M.V.R.(cm) | | | |
|----------|----------|-----|-----------|------|----------|-----|-----------|------|----------|-----|-----------|------|------------|-----|-----------|------|
| | MIN | MAX | \bar{X} | d.t. | MIN | MAX | \bar{X} | d.t. | MIN | MAX | \bar{X} | d.t. | MIN | MAX | \bar{X} | d.t. |
| Panamá | | | | | | | | | | | | | | | | |
| (n = 36) | 0.42 | 3.2 | 1.53 | 0.78 | 1.42 | 3.5 | 2.8 | 0.64 | 2.4 | 5.5 | 4.1 | 0.78 | 35 | 110 | 58.2 | 18.5 |
| Colombia | | | | | | | | | | | | | | | | |
| (n = 60) | 0.3 | 3.4 | 2.1 | 0.71 | 0.5 | 3.6 | 2.9 | 0.65 | 0.4 | 5.6 | 4.1 | 0.92 | 18.2 | 105 | 63.9 | 18.4 |

para Colombia. Las Tablas 3 y 4 muestran los valores del coeficiente de correlación, del t . calculados y los grados de significancia para los parámetros anteriores. Obsérvese sobre los mismos que todos los valores de correlación a pesar de ser positivos no son altos con excepción de la combinación L.C. x P.C. equivalente a 0.984 (98.4%), para Panamá y 0.735 (73.5%), para Colombia.

Sobre las matrices, se puede notar que los valores de correlación fueron mas altos para Panamá, excepto para P.C. x M.V.T. y L.C. x M.V.T. que fueron mayores para Colombia, lo que posiblemente se debe a las diferencias de las condiciones ambientales reinantes en las áreas de estudio.

Cleptoparásitos y otros simbioses en la tela.—Los cleptoparásitos propiamente dichos se encontraron asociados principalmente a hilos o en diminutas telas adyacentes a la de *Linothele* a donde se desplazan sobre su plataforma horizontal, bien al sentir vibraciones correspondientes a presas o residuos que fueran capturados por la araña residente. Cuando un objeto no vivo o bien algún animal vivo caían bruscamente sobre la tela o producían algún tipo de vibración anormal, se pudo observar que los cleptoparásitos abandonan rápidamente la plataforma en busca de escondite.

Los simbioses encontrados en ambas áreas sobre la tela fue el siguiente:

Uloboridae: *Philoponella vittata* (Keyserling), *P. republicana* (Simon); *P. tingena* (Chamberlin and Ivie); *Ariston* sp.

Araneidae: *Cyclosa* sp.

Theridiidae: *Argyroides atopus* (Chamberlin and Ivie), *A. cordillera* (Exline).

Theridiosomatidae: *Theridiosoma* sp.

Tetragnathidae: *Mecynometa* sp; *Leucauge venusta* (Walckenaer)

Pholcidae: *Psilochorus* sp.

Tabla 3.—Valores de la matrix de correlación para los parámetros peso y largo corporal; diámetro del orificio de la tela y mayor valor de la tela, tomado entre su largo y su ancho. P = Significancia para el valor de t calculado. Para area Colombia.

| n = 60 | P.C | P | L.C. | P | D.O | P | M.V.t. | P |
|--------|-----|---|----------|--------|---------|--------|---------|--------|
| P.C | — | — | 0.735 | | 0.323 | | 0.387 | |
| | | | t = 8.28 | <0.005 | t = 2.6 | <0.01 | t = 3.2 | <0.005 |
| L.C | | | — | — | 0.497 | | 0.523 | |
| | | | | | t = 4.4 | <0.005 | t = 4.7 | <0.005 |
| D.O | | | | | — | — | 0.353 | |
| | | | | | | | t = 2.9 | <0.005 |
| Tela | | | | | | | — | — |

Tabla 4.—Valores de la matrix de correlación para los parámetros peso y largo corporal; diámetro del orificio de la tela y mayor valor de la tela tomado entre su largo y su ancho. $N = 36$. P = Significancia para el valor de t calculado. Para area Panamá.

| | P.C | P | L.C | P | D.O | P | M.V.t. | P |
|------|-----|-----|-------------|----------|-----------|----------|------------|----------|
| P.C | — | — | 0.984 | | 0.743 | | 0.244 | |
| | | | $t = 17.37$ | <0.005 | $t = 6.5$ | <0.005 | $t = 1.47$ | N.S. |
| L.C | | | — | — | 0.728 | | 0.286 | |
| | | | | | $t = 6.2$ | <0.005 | $t = 1.74$ | <0.005 |
| D.O | | | | | — | — | 0.552 | |
| | | | | | | | $t = 3.86$ | <0.005 |
| Tela | | | | | | | — | — |

Mysmenidae: *Mysmenopsis dipluramigo* (Platnick and Shadab); *Mysmenopsis* sp.

Symphytognathidae: *Curimagua* sp.

Thomisidae: *Misumenoides* sp.

Salticidae: *Lyssomanes* sp.

Algunos ejemplares de Lycosidae, Salticidae y Linyphiidae no fueron identificados.

Las familias mejor representadas correspondieron a Ulboridae y Theridiidae por su predominante presencia en ambas áreas, pero especialmente a nivel de bosque, las especies de *P. republicana* seguida de *A. atopus* consideradas como verdaderas cleptoparásitas en la tela de *Linothele*. A muchas especies o géneros de otras familias se les consideró simbioses ocasionales ya que podían aprovechar la tela para capturar pequeñas fuentes tróficas que pasarían desapercibidas para las Dipluridae.

Vollrath (1978, 1979a, 1979b) y Rypstra (1981), estudiando la posible función de los cleptoparásitos en la tela de ciertas arañas tejedoras encontraron que fuera de limpiarla de detritos o presas dejadas por la araña huésped, eran capaces de diferenciar tipos de vibraciones producidas por ésta durante un acto de captura de presa, monitorear sus movimientos sobre la tela y así aprovechar sus descuidos para hurtarse algunas pequeñas presas inactivas.

Como Walcott (1959) lo demostró, la capacidad de ubicar la presa sobre la tela u otros agentes inductores de vibraciones, es prácticamente dependiente de sus receptores tarsales sin los cuales aún la capacidad de discriminar será afectada y de allí la importancia del acicalamiento de estos segmentos de sus miembros.

Otros organismos fueron considerados como asociados ocasionales, al encontrarse con muy baja frecuencia en algunas de las telas. Tales grupos fueron: Falangida, Hemíptera, Coleótera, Quilopoda y larvas de Lepidoptera. De estos, fue casi constante la presencia de un diminuto hemíptero de la familia Reduviidae *Metapterus* sp., caracterizado por su gran semejanza con los fasmátides, por lo cual se confunde con esos Orthoptera.

Fuentes tróficas.—De acuerdo con nuestras observaciones directas e indirectas a través de restos de alimento, las fuentes tróficas de estas arañas suelen ser muy variadas. Así, tenemos las siguientes bien en su fase adulta o larvaria: Orthoptera adultos (Blattidae y Grillidae), Hemíptera adultos, Hymenoptera adultos, Lepidoptera (principalmente larvas), pequeños Coleoptera, Isopoda (Crustácea), Diplopoda, otras arañas y aún pequeños saurios (largartija) y anuros (sapos y ranas). De estos grupos las presas más abundantes encontradas durante las horas

nocturnas correspondió a ejemplares de Blattidae, *Grillus*, larvas de Lepidoptera. Hemiptera e Hymenoptera adultos nocturnos.

Comportamiento de captura de la presa.—El comportamiento de captura de la presa suele variar y por ende las unidades de secuencia del etograma con marcadas diferencias dependiendo del tipo de la fuente trófica, por lo cual se deduce que estas arañas suelen discriminar presas vivas en concordancia con el patrón de vibraciones que produzcan como ha sido demostrado por Parry (1965) y Vollrath (1979a), o induciendo estas con artefactos mecánicos.

Para su corroboración, se experimentó con varios tipos de presas a diferentes horas, entre las 0800 y las 2000, cada día de campo, dedicando el tiempo que fuese necesario de observación para cada uno de los 25 ensayos hechos con cada presa.

Estas diferencias de conducta durante la captura de presas, se pueden observar en las Figs. 13-16 donde la frecuencia de las unidades en relación a su secuencia suele variar y el espesor de los vectores en los etogramas, representa la mayor o menor frecuencia de repetición de las unidades de actividad.

La Fig. 13 está relacionada con la captura de un Hymenóptera (avispa), en donde la araña trata de inactivar la presa con una mordida prolongada y cuando la suelta, la toca con sus miembros anteriores suavemente, mordiéndola de nuevo si la detecta viva antes de iniciar su digestión. Esto podría atribuirse a que la araña pareciera reconocer que la presa presenta un mecanismo defensivo (aguijón venenoso) altamente efectivo y trata de evitar sus consecuencias.

Las Figs. 14 y 15, ambas pertenecientes a presas de Orthoptera, se caracterizan por su mayor complejidad en unidades de secuencias de actividad. En ambas, igual que en las Figs. 13 y 16 nótese que la conducta de inactivar la presa envolviéndola primero no se presenta, a pesar que en algunos casos se observó que luego de morder, trata de envolverlas.

La Fig. 15 muestra un mayor número de unidades de secuencias, que diferencian este etograma del 14, posiblemente debido a la conducta de la araña frente a una presa con gran número de procesos espinosos sobre sus patas, dispositivos que podrían lesionar al delicado tegumento de la araña. Por esta razón posiblemente también ocurre su inactivación tratando de envolverlo en tela, lo que es poco común durante la captura de presa en representantes de la familia Dipluridae. La Fig. 16 está relacionada con la captura de una presa que se caracteriza por tener un exosqueleto altamente queratinizado y calcificado (diplópodos), lo que podía ser una de las posibles causas de que estos artrópodos no sean edibles presas para las arañas, complementado por la acción de las glándulas repugnatorias de los mismos.

El tiempo de ingestión y digestión suele variar de acuerdo con el tamaño y naturaleza de la presa, del estado fisiológico de la araña y de si la captura se hace sobre una tela terminada o en construcción.

No es normal encontrar en el interior de la cueva o sobre la tela, restos de presas ya que estas arañas sacan sus residuos al terminar el proceso ingestivo y digestivo, cuyas partes blandas aún presentes, suelen ser aprovechadas por otros organismos, especialmente hormigas.

Actividad agonística.—La interacción agonística se manifiesta con arañas del mismo género y diferentes especies, por ejemplo; si una *Linothele* sp. considerada como intrusa se coloca sobre la tela de otra (residente), la primera puede quedarse inmóvil inicialmente para luego huir, o huir inmediatamente al ser

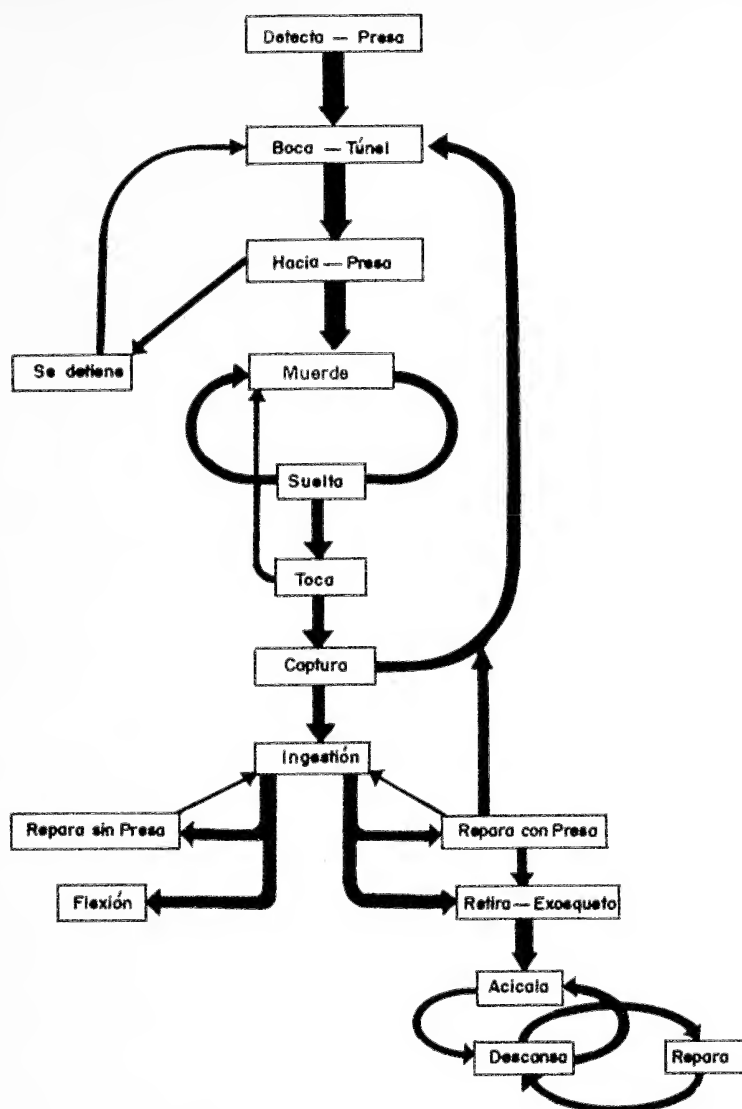


Fig. 13.—Patrón de secuencia de unidades del comportamiento de captura de un Hymenoptera (Avispa). El espesor de los vectores indica la frecuencia con que se repitió una actividad.

perseguida por la residente, la que en caso de capturarla será predada. Es de resaltar que aunque la intrusa sea de mayor tamaño que la residente, no suele manifestar agresividad a esta última, cosa que sí exhibe la residente. Este patrón de comportamiento se pudo observar con intrusas de diferentes géneros colocándolos con la mano sobre la red de la residente y en terrarios tales como: *Argiope*, *Nephilla*, *Gasteracantha*, *Leucauge*, *Micrathena*, *Lycosa* y otras Dipluridae.

Si en condiciones de laboratorio se juntan dos arañas de igual tamaño en un terrario, estas exhiben acciones agonísticas entre sí y cualquiera de las dos podrá ser la víctima. Pero en caso de que una de ellas inicie la construcción de su nido primero que la otra, aquella por lo general se torna más agresiva y normalmente

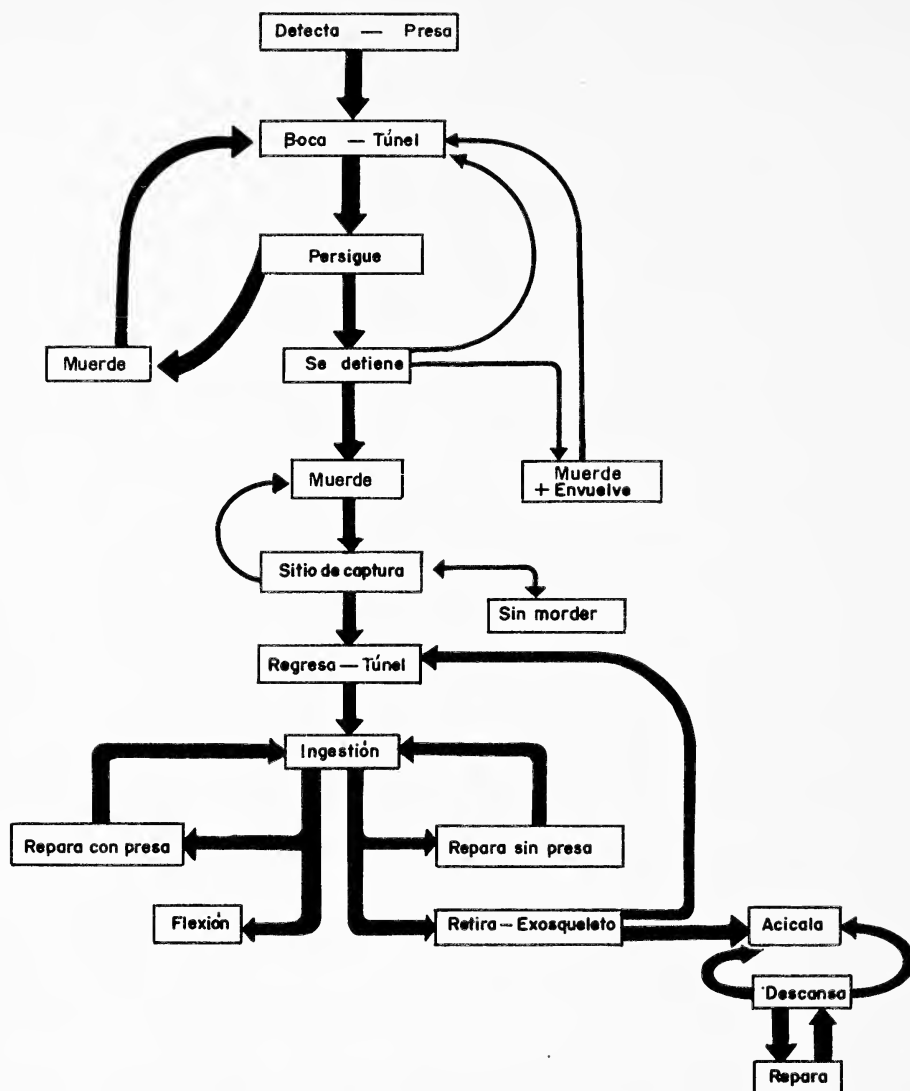


Fig. 14.—Patrón de secuencia de unidades del comportamiento de captura de una Blattidae (*Periplaneta americana*), por *Linothele* sp. El espesor de los vectores indica la frecuencia con que se repitió una actividad.

mata a la compañera. Si hay diferencia de madurez sexual la araña más adulta normalmente mata a la más joven.

Sin embargo, esta conducta puede variar si se juntan machos y hembras inmaduros o hembras entre sí inmaduras, en donde ambos ejemplares manifiestan actividad agonística sin llegar al acto de predación pudiendo convivir durante mucho tiempo.

Esta situación también se modifica si a una hembra sexualmente madura pero no receptiva se le agrega un macho inmaduro o adulto. En ambos casos suele devorarlos, no así si la hembra está receptiva y el macho sexualmente maduro; en este último caso hay acciones agonísticas dentro de los movimientos de galanteo

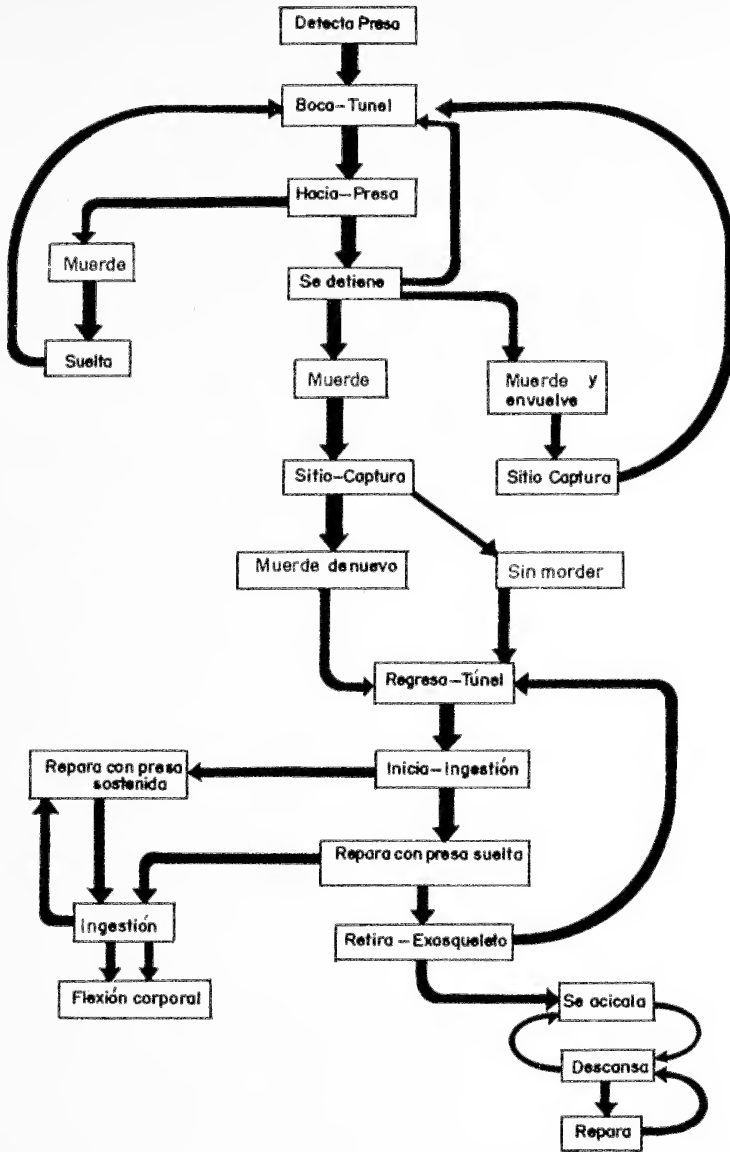


Fig. 15.—Patrón de secuencia de unidades del comportamiento de captura de un Orthoptera (Grillos), por *Linothele* sp. El espesor de los vectores indica la frecuencia con que se repitió una actividad.

precopulatorio pudiendo convivir en el mismo recipiente por varios días con el macho aunque este carezca de espermátóforos en sus palpos.

La agresividad entre estas arañas es muy posible que dependa del número de mudas padecidas por los ejemplares ya que mientras más inmaduras eran las arañas menor fue la expresión de agresividad entre ellas y mientras más próxima a su madurez sexual mayor era esta expresión agonística, lo cual espero corroborar en la segunda fase del estudio relacionado sólo con la biología reproductiva y desarrollo postembrionario de las mismas.

De nuestras observaciones con estas Dipluridae se puede deducir que las mismas no contruyen realmente sus cuevas, como sí lo hacen otras familias del

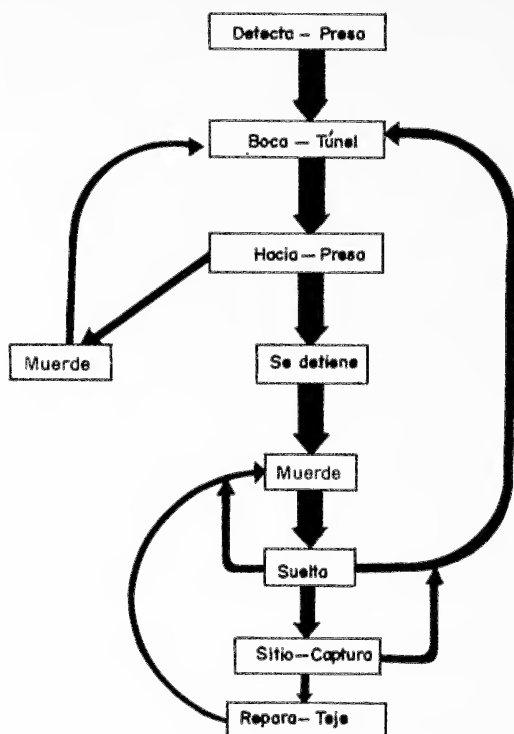


Fig. 16.—Patrón de secuencia de unidades del comportamiento de captura de un Diplopoda carinado (*Polidesmus* sp.). El espesor de los vectores indica la frecuencia con que se repitió una actividad.

orden aunque existe la posibilidad de que si el terreno lo permite modifique algunos sectores de la depresión natural, lo que representaría para estas especies una gran ventaja desde el punto de vista de costo energético en relación a aquellas que sí construyen su depresión como en Ctenizidae (Coyle 1981) Lycosidae, Theraphosidae y algunos de Dipluridae del área australiana (Main 1975, 1982).

La pobre capacidad migratoria de estas arañas favorece algunas hipótesis de la función de ser territorial concebida por algunos autores y de manera especial en la revisión del concepto por Verner (1977) tales como aprovechar recursos y material de nidación, impedir el contagio de enfermedades, aumentar la posibilidad de neutralizar acciones predatoras, de selección de pareja o de tener éxito reproductivo y disminuir las interacciones agonísticas intra e interespecíficas.

Sin embargo, de acuerdo con lo observado, la riqueza en fuentes tróficas no parece ser uno de los parámetros vitales del gran poder de residencia de estas arañas ya que se encontraron muchas telas en sitios bastante pobres en fuentes de alimentos aún durante la noche y además, como se pudo demostrar en condiciones de cautiverio (no alimentadas por más de dos meses), estas arañas suelen soportar largos períodos sin comer, especialmente en la época de muda. Por lo tanto, la escasa abundancia de presas tampoco sería causa de abandono de las telas.

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CONTRIBUCIÓN AL CONOCIMIENTO TAXONÓMICO DEL GÉNERO *UROPHONIUS* POCKOCK, 1893 (SCORPIONES, BOTHRIURIDAE)¹

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ABSTRACT

In this paper, three species-groups within the genus *Urophonius* are recognized: *exochus* group, *granulatus* group and *brachycentrus* group. The diagnostic characters used at this level are: arrangement of ventral submedian carinae in metasomal segment I; ventral chaetotaxy in metasomal segments I, II and III; telotarsal spine formula (legs III and IV); morphology of lobe region of hemispermatophore; relative location of femur trichobothria *d* and *e*, and macrosetae M1 and M2; ventral pigmentation pattern of metasoma. A key for the nominate species in the genus, as well as some comments on distribution and bioecology, are added.

RESUMEN

Se reconoce la existencia de tres grupos de especies dentro del género *Urophonius*: grupo *exochus*, grupo *granulatus* y grupo *brachycentrus*. Los caracteres diagnósticos empleados a este nivel son: disposición de carenas ventrales submedianas en segmento caudal I; chaetotaxia ventral en segmentos caudales I, II y III; fórmula de espinulación telotarsal (patas III y IV); morfología de la región de lóbulos del hemispermatóforo; posición relativa de las tricobotrias femorales *d* y *e*, y las macroquetas M1 y M2; patrón de pigmentación ventral en metasoma. Se incluyen una clave para las especies nominadas del género, así como algunos comentarios sobre distribución y bioecología.

INTRODUCCION

Entre los géneros de Bothriuridae más difíciles para su estudio taxonómico se encuentra *Urophonius* Pocock, 1893. Las dificultades de hallar caracteres diagnósticos seguros en el nivel específico llevaron a frecuentes confusiones de los investigadores, quienes ya a fines del siglo pasado, cuando el género contaba apenas con tres especies nominadas, tenían problemas para distinguir dos de ellas -*U. brachycentrus* (Thorell, 1877) y *U. jheringii* Pocock, 1893, durante largo tiempo considerados como sinónimos-; también *U. granulatus* Pocock, 1898 fue motivo de controversias, ya que, como lo señala Maury (1979), "ha pasado por lo menos bajo 5 denominaciones distintas". El posterior aumento del número de

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especies, en algunos casos injustificado, complicó el panorama, en tanto similar efecto tuvo un artículo de San Martín (1965), en el que, tras proponer acertadamente la sinonimia genérica de *Urophonius* con *Iophorus* Penther, 1913, designa a ejemplares de *U. granulatus* como "alotipo" y "paratipo macho" de *U. eugenicus* (Mello-Leitão, 1931) (Maury, 1979).

Un primer intento de aclarar la situación corresponde a Maury (1973), que postula la subdivisión del género en dos "grupos de especies", basándose principalmente en la fórmula de espinulación telotarsal. Entiendo que tal división es válida parcialmente, pues, si bien el denominado "grupo A" incluye especies claramente afines (equivale al concepto de *Iophorus*), no ocurre lo mismo con el "grupo B", en el cual pueden distinguirse al menos dos grupos diferentes. En un segundo aporte, sin volver a referirse a tales grupos, Maury (1977) menciona una serie de caracteres que considera adecuados para la identificación de las especies. Dichos caracteres -y otros que deben añadirse- pueden ser jerarquizados, siendo algunos de ellos útiles para distinguir grupos de especies, como veremos, en tanto otros sólo tienen valor a nivel específico.

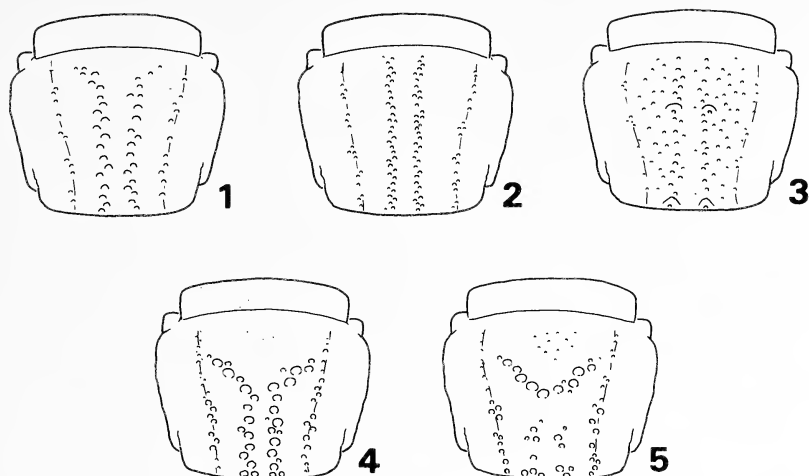
Luego de estudiar las especies conocidas del género -excepto *U. tumbensis* Cekalovic, 1981-, he comprobado que es posible reunir las en tres grupos, a los que he denominado con el nombre de su especie más característica: grupo *brachycentrus*, grupo *granulatus* y grupo *exochus* (este último coincide con el "grupo A" de Maury, 1973); para su distinción he tomado en cuenta una serie de siete caracteres, a los que me referiré en el punto siguiente. La ubicación de *U. tumbensis* en alguno de estos grupos, así como su inclusión en la clave que acompaña este trabajo, quedan pendientes, por cuanto no he podido examinar ningún ejemplar de dicha especie, y los datos proporcionados en la descripción original son insuficientes.

Aunque los aquí propuestos son, sin duda, auténticos grupos naturales -probablemente representan sendas líneas filogenéticas-, la magnitud de las diferencias no parece ser suficiente para otorgarles categoría subgenérica. Por de pronto, su reconocimiento podrá servir de orientación en el esclarecimiento sistemático de un género tan homogéneo como lo es *Urophonius*.

CARACTERES UTILIZADOS

Los grupos de especies de *Urophonius* pueden reconocerse por los siguientes caracteres: (1) carenas ventrales submedianas del segmento caudal I; (2) disposición de quetas ventrales en el mismo segmento; (3) disposición de dichas quetas en los segmentos caudales II y III; (4) espinulación telotarsal en patas III y IV (fórmula más frecuente); (5) morfología de la región de lóbulos en el hemiespermatóforo; (6) posición de las tricobotrias *d* y *e* en el fémur respecto de las macroquetas indicadas como M1 y M2 en Figs. 12 a 14; (7) patrón de pigmentación ventral en el metasoma. La nomenclatura que empleo para las carenas caudales responde a lo propuesto por Francke (1977), mientras la correspondiente a los lóbulos del hemiespermatóforo es la utilizada por San Martín (1963); las siglas tricobotriales han sido tomadas de Vachon (1973). En cuanto a las macroquetas del fémur referidas en el carácter 6, su denominación es arbitraria, al solo efecto de su individualización en las figuras.

De los caracteres considerados, la morfología de la región de lóbulos del hemiespermatóforo es sin duda el más importante. En el género *Urophonius* el



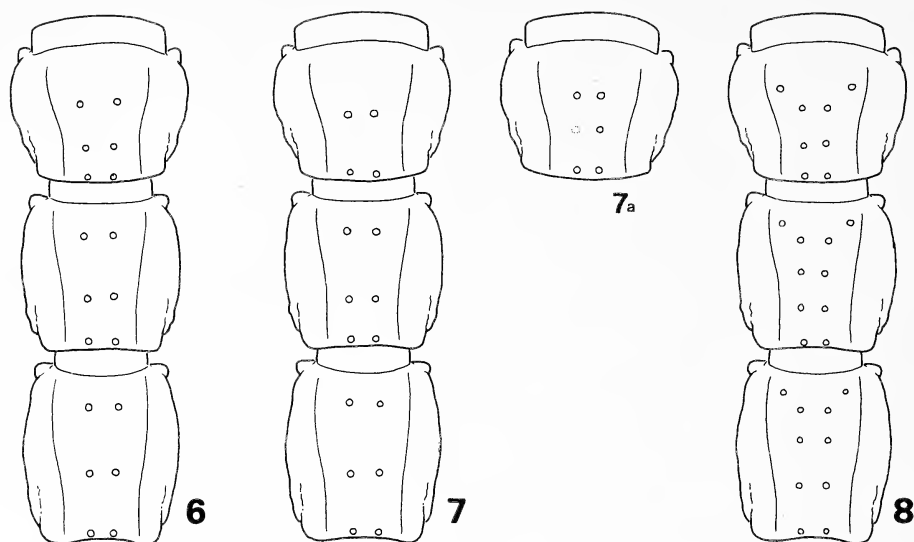
Figs. 1-5.—Carenas ventrales submedianas del segmento caudal I: 1, grupo *exochus*; 2-3, grupo *granulatus*; 2, *Urophonius granulatus*; 3, otras especies; 4-5, grupo *brachycentrus*; 4, *Urophonius* sp. (Chile central); 5, otras especies.

hemiespermatóforo responde, en vista externa, a un único modelo básico, donde pequeñas variaciones en la lámina distal y las apófisis representan diferencias específicas (Maury, 1980). Por el contrario, el estudio de la región de lóbulos -en vista interna- permite reconocer la existencia de tres patrones bien definidos (correspondientes a cada grupo de especies), según el distinto desarrollo de los pliegues formados entre el lóbulo interno (l.i.) y el lóbulo basal (l.b.), y entre éste y el lóbulo externo (l.e.); es también importante la presencia y morfología de una prolongación laminar en el extremo del l.b.

Es de notar que ninguno de los caracteres restantes puede ser empleado individualmente para una separación categórica de los tres grupos de especies, y por este motivo deben tomarse necesariamente en su conjunto. Otros caracteres (tales como la forma del telson, el número de dientes pectíneos, los diseños cromáticos de prosoma y tergitos, etc.), subordinados a los que se emplean en este trabajo, o bien estados particulares de éstos, permiten la distinción de las especies, pero con diferente valor dentro de cada grupo. El presente artículo incluye una clave para diferenciar las especies nominadas de *Urophonius*, donde se hace mención de estos caracteres del nivel específico.

GRUPO *EXOCHUS*

Diagnosis.—Segmento caudal I: carenas ventrales submedianas longitudinales, algo divergentes en su extremo proximal (Fig. 1); tres pares de macroquetas ventrales, siguiendo las carenas (Fig. 6). Segmentos II y III: tres pares de macroquetas (Fig. 6); puede haber un par de microquetas proximales, cercano a los laterales. Espinulación telotarsal: T III: 4-4, T IV: 4-5. Hemiespermatóforo con la región de lóbulos bien desarrollada, particularmente el pliegue formado entre l.i. y l.b., mientras el sector entre l.b. y l.e. es apenas una angosta franja (Fig. 9); el lóbulo basal carece de prolongación laminar evidente, pero existe una estructura laminar rudimentaria oculta tras el propio lóbulo, quizás equivalente a las prolongaciones presentes en otros grupos. Entre tricobotrias *d* y *e* del fémur



Figs. 6-8.—Quetotaxia ventral de los segmentos caudales I a III: 6, grupo *exochus*; 7, grupo *granulatus*; 7a, *Urophonius tregualemuensis*; 8, grupo *brachycentrus*.

aparece una sola macroqueta (M1, Fig. 12), equidistante de ellas. Pigmentación ventral en metasoma: dos bandas paramedianas irregulares.

Especies incluidas y distribución.—*Urophonius exochus* (Penther, 1913).

Argentina: Mendoza, Neuquén, ¿Río Negro?

Urophonius eugenicus (Mello-Leitão, 1931). Argentina: Santa Cruz.

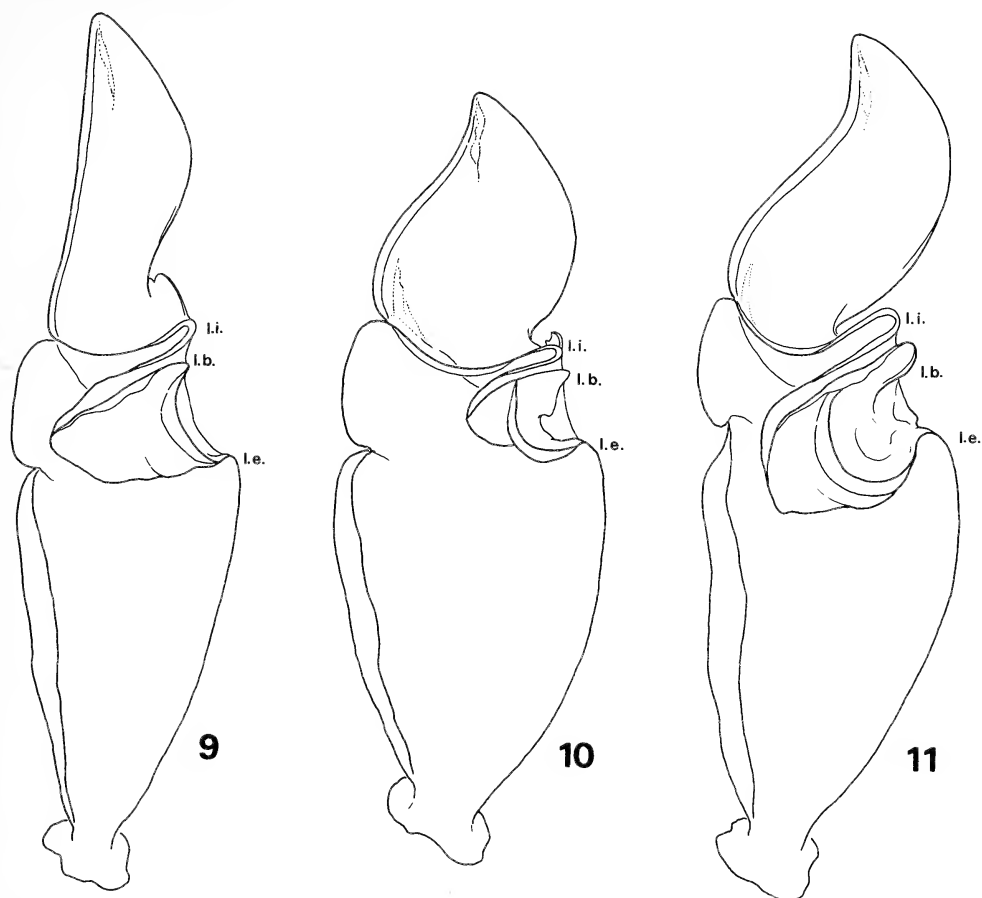
Urophonius mahuidensis Maury, 1973. Argentina: sur de Buenos Aires, norte de Río Negro.

Urophonius sp.: una forma posiblemente innominada de Perito Moreno (provincia de Santa Cruz, Argentina).

Comentarios.—Si bien este grupo es inconfundible como tal, persisten dudas a nivel específico, por la ausencia de caracteres diacríticos seguros. El estudio del hemiespermatóforo parece confirmar la validez de estas especies, a pesar de su gran semejanza externa.

GRUPO *GRANULATUS*

Diagnosis.—Segmento caudal I: carenas ventrales submedianas longitudinales, bien definidas (Fig. 2) o con sus gránulos dispersos (Fig. 3); dos pares de macroquetas ventrales (Fig. 7), menos frecuentemente tres pares, en este último caso puede faltar una queta del par medio (Fig. 7a). Segmentos II y III: tres pares de macroquetas (Fig. 7); pueden agregarse un par de microquetas proximales. Espinulación telotarsal: T III: 5-5, 5-6, T IV: 5-6, 6-6 (6-7). Hemiespermatóforo con región de lóbulos poco extendida; el l.b. se resuelve en una estructura laminar plana muy evidente, de borde característico (Fig. 10); sector entre l.b. y l.e. cóncavo. Tricobotria *e* del fémur próxima a la única macroqueta (M1, Fig. 13), pero de posición variable según la especie. Pigmentación ventral en metasoma: banda axial y lateroventrales nítidas, paramedianas ausentes.



Figs. 9-11.—Hemiespermatóforo izquierdo, en vista interna: 9, grupo *exochus* (*Urophonius mahuidensis*); 10, grupo *granulatus* (*U. granulatus*); 11, grupo *brachycentrus* (*U. jheringii*), l.i. = lóbulo interno, l.b. = lóbulo basal, l.e. = lóbulo externo.

Especies incluidas y distribución.—*Urophonius granulatus* Pocock, 1898 = *Iophoroxenus exilimanus* Mello-Leitão, 1932 = *U. paynensis* San Martín y Cekalovic, 1968. Argentina: Santa Cruz, Chubut; sur de Chile.

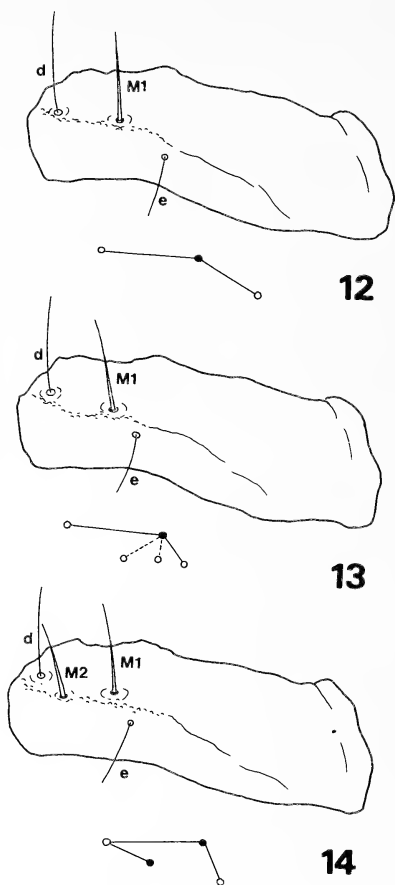
Urophonius tregualemuensis Cekalovic, 1981. Chile central.

Urophonius sp.: Meseta de Somuncurá (provincia de Río Negro, Argentina).

GRUPO *BRACHYCENTRUS*

Diagnosis.—Segmento caudal I: carenas ventrales submedias longitudinales en su extremo distal, toman una orientación bruscamente oblicua y divergente en la mitad proximal del segmento (Fig. 4); con frecuencia las ramas oblicuas se conectan en la línea media, separándose de las primitivas carenas longitudinales para formar una única carena transversal (Fig. 5); gránulos por lo general perliformes y conspicuos; cuatro pares de macroquetas ventrales, el par proximal sigue la dirección de las carenas, ubicándose cerca de los laterales (Fig. 8). Segmentos II y III: siempre más de tres pares de macroquetas ventrales (entre cuatro y seis pares), el proximal se acerca a los laterales (Fig. 8). Espinulación

Figs. 12-14.—Posición relativa de tricobotrias *d* (dorsal) y *e* (externa), y macroquetas M1 y M2 en fémur derecho: 12, grupo *exochus*; 13, grupo *granulatus*; 14, grupo *brachycentrus*. En cada grupo, debajo del dibujo correspondiente, se ha graficado en forma esquemática la relación entre las tricobotrias (círculos blancos) y las macroquetas (círculos negros); la tricobotria *e* en el grupo *granulatus* puede tomar posiciones diferentes, según la especie.



telotarsal: T III: 5-6, 6-6, T IV: 6-6, 6-7. Hemiespermatóforo con región de lóbulos bien desarrollada y compleja; la concavidad ubicada entre l.b. y l.e. está muy extendida, ocultando buena parte del pliegue formado entre el l.i. y el propio l.b.; este último termina en una conspicua estructura laminar, de bordes curvados y suavemente cóncava (Fig. 11). Próxima a la tricobotria *d* del fémur aparece una nueva macroqueta (indicada como M2 en Fig. 14). Pigmentación ventral en metasoma: un par de bandas paramedianas longitudinales, de borde irregular, que pueden estar acompañadas de un esbozo de banda axial, o confluir en la línea media.

Especies incluidas y distribución.—*Urophonius brachycentrus* (Thorell, 1877).

Argentina; Córdoba, sur de Santiago del Estero, La Rioja, Tucumán, llegando hasta Entre Ríos, La Pampa, norte y sur de Buenos Aires.

Urophonius jheringii Pocock, 1893 = *U. corderoi* Mello-Leitão, 1931 = *U. granulosisissimus* Mello-Leitão, 1934. Argentina: sierras de Tandil y Ventana (provincia de Buenos Aires); Uruguay; sur de Brasil.

Urophonius achalensis Abalos y Hominal, 1974. Argentina: piso altitudinal superior en las Sierras Grandes (provincia de Córdoba).

Urophonius sp.: Chile central.

CLAVE PARA LAS ESPECIES NOMINADAS DE *UROPHONIUS*

1. Carenas ventrales submedianas del segmento caudal I longitudinales; dos o tres pares de quetas ventrales en dicho segmento, tres pares en los segmentos II y III. Región de lóbulos del hemiespermatóforo poco desarrollada, o al menos sólo desarrollado el pliegue entre l.i. y l.b. Tricobotrias *d* y *e* del fémur relacionadas con una única macroqueta.....2
- Carenas ventrales submedianas del segmento caudal I transversales en la mitad proximal del artejo; superficie ventral del mismo segmento con cuatro pares de quetas, siguiendo las carenas, y con más de tres pares en los segmentos II y III. Región de lóbulos muy desarrollada; l.b. con prolongación laminar cóncava. Tricobotrias *d* y *e* del fémur relacionadas con dos macroquetas. Espinulación telotarsal: T III: 5-6, 6-6, T IV: 6-6, 6-7. Grupo *brachycentrus* 6
2. Espinulación telotarsal: T III: 4-4, T IV: 4-5. Región de lóbulos del hemiespermatóforo con gran desarrollo del pliegue entre l.i. y l.b., y escaso de la concavidad entre l.b. y l.e.; l.b. sin prolongación laminar. Superficie ventral del metasoma provista de dos bandas de pigmento paramedianas y dos lateroventrales poco definidas, de bordes irregulares. Segmento caudal I con tres pares de quetas ventrales. Tricobotrias *d* y *e* equidistantes de la única macroqueta (M1). Grupo *exochus*.....3
- Espinulación telotarsal: T III: 5-5, 5-6, T IV: 5-6, 6-6 (6-7). Región de lóbulos del hemiespermatóforo pequeña; l.b. con prolongación laminar plana. Superficie ventral del metasoma con dos bandas de pigmento lateroventrales y una axial, bien definidas. Segmento caudal I con dos o tres pares de quetas ventrales. Tricobotria *e* más cerca de la macroqueta M1 que la tricobotria *d*. Grupo *granulatus*.....5
3. Hemiespermatóforo con lámina distal delgada; l.i. con protuberancia bifida cercana a la base de la lámina distal. Telson bajo.....4
- Hemiespermatóforo con lámina distal ancha; protuberancia bifida del l.i. alejada de la base de la lámina distal. Telson alto.....*U. eugenicus*
4. Lámina distal del hemiespermatóforo recta; protuberancia bifida unida a la base de la lámina distal.....*U. mahuidensis*
- Lámina distal del hemiespermatóforo suavemente curva; protuberancia bifida sin conexión con la base de la lámina distal.....*U. exochus*
5. Carenas ventrales submedianas del segmento caudal I bien definidas; dos pares de quetas ventrales. Carenas ventrales laterales del segmento caudal V bien definidas. Tricobotria *e* en posición más distal que la macroqueta M1. Hemiespermatóforo sin repliegue distal posterior, y con lámina distal ancha; l.i. con protuberancia bifida en su borde externo.....*U. granulatus*
- Carenas ventrales submedianas del segmento caudal I algo dispersas hacia los laterales en una zona granulosa; tres pares de quetas ventrales (puede faltar una del par medio). Carenas ventrales laterales del segmento caudal V poco definidas hacia proximal. Tricobotria *e* en posición más proximal que la macroqueta M1. Hemiespermatóforo con repliegue distal posterior y lámina distal delgada; l.i. con un denticulo en su cara externa....*U. tregualemuensis*
6. Carenas ventrales laterales y ventral mediana del segmento caudal V presentes sólo en el tercio posterior. Surco interocular suave. Diseño cromático de la

- superficie ventral del metasoma: manchas paramedianas muy extendidas, por lo general confluyen en la línea media. Macho con pinzas comparativamente más gruesas. Hemiespermatóforo con lámina distal gruesa, repliegue distal posterior bien desarrollado; l.i. con un par de denticulos en su cara externa. Número de dientes pectíneos: macho, 14 a 15, hembra, 12 a 14. Superficie ventral del segmento caudal III granuloso. Carenas ventrales laterales del segmento I vestigiales..... *U. jheringii*
- Carenas ventrales laterales y ventral mediana del segmento caudal V más extendidas. Surco interocular marcado. Dimorfismo sexual en pinzas menos acentuado. Repliegue distal posterior menos desarrollado. Mayor número de dientes pectíneos. Diseño cromático de la superficie ventral del metasoma: manchas paramedianas más limitadas, no confluyen en la línea media. Carenas ventrales laterales del segmento caudal I bien desarrolladas.....7
7. Tergitos con un par de manchas paramedianas en forma de paréntesis. Número de dientes pectíneos: macho, 17 a 20, hembra, 16 a 18. Segmento caudal III granuloso por ventral. Repliegue distal posterior muy pequeño, lámina distal ancha; l.i. con protuberancia bífida en su borde externo.....
..... *U. brachycentrus*
- Tergitos con un par de manchas paramedianas subtriangulares. Número de dientes pectíneos: macho, 16 a 18, hembra, 14 a 16. Segmento caudal III liso por ventral (en algunas hembras, escasos gránulos). Repliegue distal posterior medianamente desarrollado, lámina distal delgada; l.i. con un par de denticulos en su cara externa..... *U. achalensis*

OBSERVACIONES ZOOGEOGRAFICAS Y BIOECOLOGICAS

En la Fig. 15 se indica el área de distribución conocida para cada grupo de especies de *Urophonius*. Si excluimos las especies de Chile central, es claro que el grupo *granulatus* habita un ambiente netamente patagónico, mientras el grupo *brachycentrus* se asocia básicamente a los antiguos macizos serranos peripampásicos (en el caso de *U. brachycentrus*, extendiéndose también en áreas no serranas, con vegetación tipo "espinal"). Menos definida aparece el área ocupada por el grupo *exochus*, aunque posiblemente el registro que disponemos de él es aún muy incompleto. Como hecho destacable, parece no existir simpatria de especies pertenecientes a un mismo grupo, algo que por lo visto sí sería posible entre grupos diferentes (*U. jheringii* y *U. mahuidensis* en las sierras de Tandil y Ventana; *U. granulatus* y *U. eugenicus* en Santa Cruz; *U. tregualemuensis* y *U. sp.* en Chile central). La coexistencia de *U. brachycentrus* y *U. achalensis* en las sierras de Córdoba no sería la excepción, pues en este caso se verifica una separación altitudinal, con distribución de tipo parapátrico (Acosta, en prensa). De igual modo, *U. brachycentrus* se extiende hasta proximidades de los sistemas serranos bonaerenses -habitados por *U. jheringii*- pero al parecer no penetra en ellos.

Otro aspecto que merece destacarse es la existencia en *Urophonius* de dos tipos de ciclos de actividad (Maury, 1979): algunas especies, tales como *U. brachycentrus* y *U. jheringii*, presentan un período de actividad "de superficie" fundamentalmente invernial, en tanto otras hacen su aparición en los meses de verano (por ejemplo *U. granulatus*). Maury (1979) ha señalado que el ciclo con

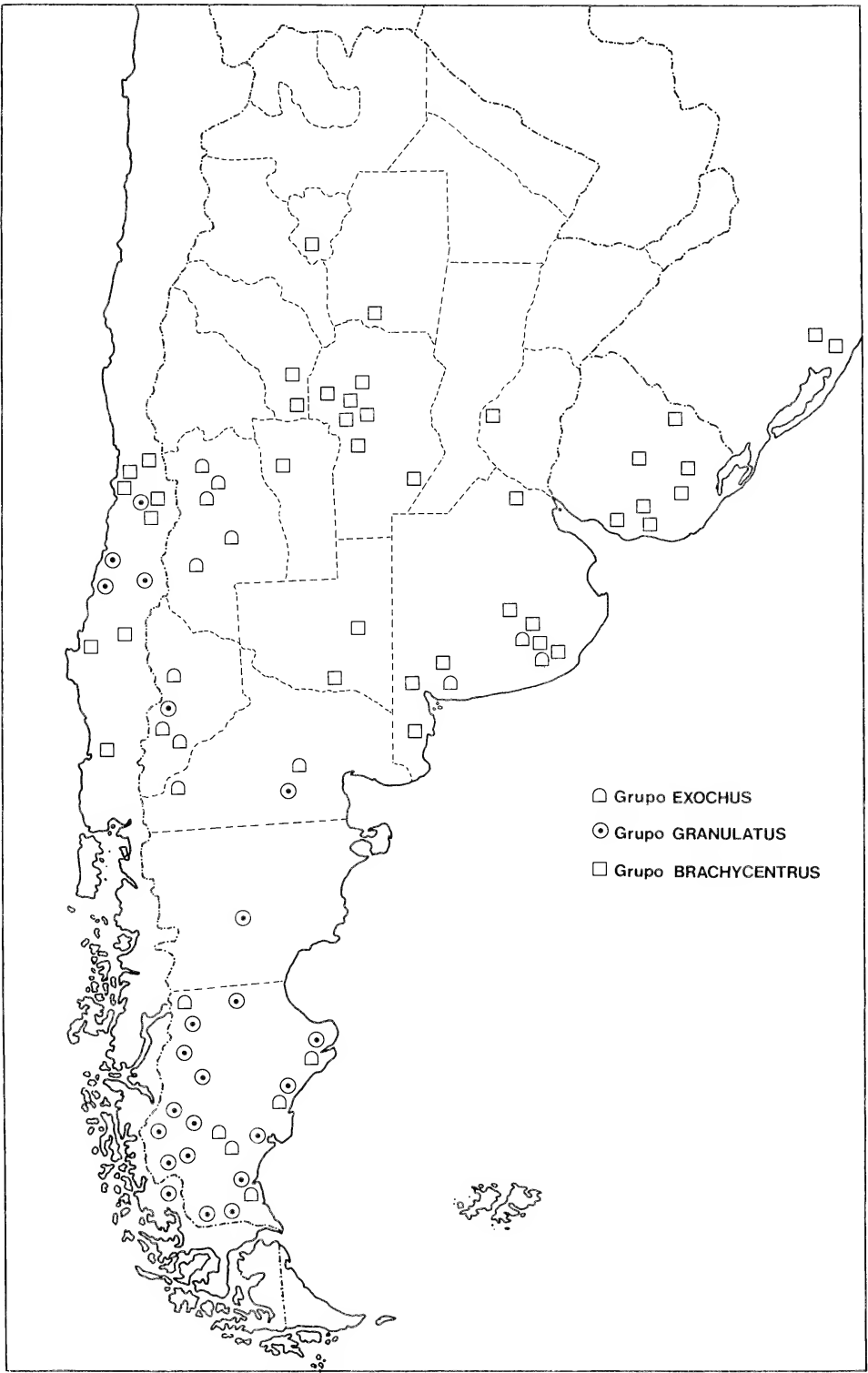


Fig. 15.—Distribución geográfica conocida de los tres grupos de especies de *Urophonius*.

actividad invernal -invertido respecto de lo común en otros Bothriuridae- puede interpretarse como una adaptación secundaria, que permitiría eludir la competencia con otros escorpiones presentes en la zona (por ejemplo, las diversas especies de *Bothriurus*). En cuanto al grupo "estival", el límite norte de su área de dispersión pasaría, según Maury (1979), próximo al paralelo 46° S, que lo confinaría prácticamente a la provincia argentina de Santa Cruz; la única excepción sería *Urophonius* sp. de la Meseta de Somuncurá, ubicada casi a 500 km al norte aunque con un ambiente similar. En rigor, el período de actividad estival, mejor que relacionado a un área geográfica dada, parece ser una característica de todas las especies del grupo *granulatus*, ya que a *U. granulatus* y *U. sp.* de Somuncurá se suma *U. tregualemuensis*, este último con capturas entre octubre y marzo (de acuerdo con el material estudiado). En contrapartida, el período invernal correspondería a las especies del grupo *brachycentrus*, lo que incluye a *Urophonius* sp. de Chile central, cuya mayor frecuencia de capturas se ubica entre abril y octubre. En el caso del grupo *exochus*, la información disponible es aún escasa, lo que impide por el momento tener una idea clara sobre las características de su ciclo.

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INTERSPECIFIC TOLERANCE IN SOCIAL *STEGODYPHUS* SPIDERS (ERESIDAE, ARANEAE)

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ABSTRACT

The African social eresid spiders *Stegodyphus mimosarum* and *S. dumicola* exhibit extreme intra- as well as interspecific social tolerance. *S. mimosarum* individuals transferred over more than 20 km were accepted and immediately cooperated in strange conspecific colonies. In a laboratory experiment, adult females of both species formed mixed-species groups that spun and fed together.

INTRODUCTION

Among higher invertebrates social life has evolved in two taxa, in spiders and in insects. In spiders, social cooperation has arisen independently in several phylogenetic groups. The published schemes for the evolution of arachnid sociality suggest that two major forces may operate: a mutualistic cooperation among related or unrelated adults, and a prolongation of bonds between siblings (Buskirk 1981). The only arboreal genus in the cribellate family Eresidae, the Indo-African spider genus *Stegodyphus*, contains solitary as well as periodically and permanently social species, suggesting a pathway for evolution of sociality within this genus (Giltay 1927; Kullman 1972). Here we report on the social tolerance of two permanently social species, *Stegodyphus mimosarum* Pavesi and *S. dumicola* Pocock from Africa.

Both species inhabit dry thornbush country, living in colonies in compact, sponge-like silk nests found mostly in thorny trees. The animals mostly rest during daylight hours. The distribution of colonies is very patchy with several km between patches. New colonies are founded by groups of nearly, or fully, adult individuals emigrating from one colony to adjacent branches and trees. In addition, single adult females "balloon" by air, presumably founding new colonies far away (Wickler and Seibt 1986).

MATERIALS AND METHODS

We observed the animals in the field and the laboratory. Colonies were collected in 1985 from Swaziland, Transvaal and Natal (South Africa). They can easily be kept indoors for about a year. We fed them flies, small crickets and flour beetles.

Tolerance tests.—To test intraspecific tolerance in the field we, on three occasions, introduced individually marked *S. mimosarum* females into foreign colonies more than 20 km away. In addition, we removed several individuals from different colonies and combined them into new groups in the laboratory.

Interspecific tolerance was studied in the laboratory. In order to avoid any bias from prior residence, we put five *S. mimosarum* and five *S. dumicola* adult females of similar size (6-7 mm in length; within a species, from the same colony) in an empty 10 × 10 × 10 cm glass cube without any of their original nest material. Three such groups were started in parallel and observed for 55 days. We took 25 records of the spiders' local position and social aggregations for each of the three groups (never more than one per day). Records were taken at random day-times, the spiders were always quiescent and without food at that time.

RESULTS

Interspecific tolerance.—In neither case did we detect differences between the contacts with strange individuals and those between colony mates. One individual introduced into a foreign colony even joined some local individuals in subduing a prey insect within 5 min. There was no indication of colony membership identification. This result was the same as obtained in earlier experiments with the same species in Tanzania (Wickler 1973).

Interspecific tolerance.—Invariably, all 10 spiders (of both species) freshly introduced into a cage formed a dense clump within 1-3 hours and remained clumped for many hours. They started spinning within one hour and the combined effort produced a silken mass. When given food, members of both species joined to subdue and consume the prey. We did not observe interspecific aggression or avoidance. In fact, all feeding groups observed were heterospecific. These groupings on food were clearly induced by the feeding situation. Since each single spider might have been attracted by the food rather than by the other spiders, these feeding groups were eliminated from the following analysis which is based on 163 records of quiescent spider groupings. The animals were offered food about once a week; their immediate responses showed that they were hungry and, therefore, not tolerant just by satiation. Table 1 shows the frequencies of homo- and heterospecific groupings that occurred during the experiment.

All 10 individuals in a cage were clumped in 27 (= 31.4%) of the 86 heterospecific groupings, forming a dense ball with maximal bodily contact. This illustrates the strong thigmotactic tendency of these spiders. Although isolated spiders of either species would attempt maximal bodily contact with any substrate (thus coming to rest in corners, fissures of bark, etc.), other *Stegodyphus* individuals regardless of species are more attractive. This is an expression of the "interattraction" typical for social spiders (Darchen 1965).

Single spiders resting isolated from the other cagemates were recorded 58 times; in 45 cases it was a *S. dumicola*, in 13 cases a *S. mimosarum*. The difference is significant at $p < 0.01$ (binomial test) and may have resulted from *S. dumicola*'s higher locomotory activity.

Six or more individuals were found in 65 aggregations. These necessarily contained both species. In addition, 21 groups of less than six individuals contained members of both species (Table 1). Thus, heterospecific groups were

Table 1.—Frequencies of observed homo- and heterospecific groupings of *Stegodyphus dumicola* and *S. mimosarum* during 55 days.

| Group size | Homospecific | | Heterospecific |
|------------|--------------------|---------------------|----------------|
| | <i>S. dumicola</i> | <i>S. mimosarum</i> | |
| 1 | 45 | 13 | |
| 2 | 3 | 8 | 4 |
| 3 | 4 | 1 | 9 |
| 4 | 0 | 1 | 4 |
| 5 | 1 | 1 | 4 |
| 6 | | | 10 |
| 7 | | | 9 |
| 8 | | | 4 |
| 9 | | | 15 |
| 10 | | | 27 |

not a mere side effect caused by a tendency to congregate in larger groups (of more than five individuals). Groups of two to five individuals were heterospecific in 21 and homospecific in 19 cases (8 of *S. dumicola*, 11 of *S. mimosarum*), showing no apparent tendency of either species to aggregate separately.

The presence of *Stegodyphus* silk seems to attract individuals of either species. Searching individuals that come across a silk strand will follow it; texture and/or pheromones may be relevant cues. But two individuals, again regardless of species, coming from different directions on a completely clean surface, will contact each other in the typical manner without even touching the other's security thread.

DISCUSSION

In the field we observed intermigration between separate (presumably daughter-) colonies of both species over distances less than 10 m. Bradoo (1972) reports the same phenomenon for *S. sarasinorum* Karsch from India. To exclude familiarity between closely neighboring groups, we mixed individuals from far distant colonies. In all cases foreign individuals were tolerated in any conspecific colony. Kullmann (1968) and Bradoo (1980) obtained the same results for *S. sarasinorum*. Thus there seems to be no colony integrity in social *Stegodyphus* spiders.

Interspecific inter-colony tolerance has also been reported in the social spiders *Agelena consociata* Denis and *A. republicana* Darchen (Agelenidae), *Metabus gravidus* Cambridge (Araneidae), *Anelosimus eximus* Simon and *A. studiosus* Hentz (Theridiidae) and in *Mallos gregalis* Simon (Dictynidae) (Buskirk 1981), that is in all social species that have been so tested. Social spiders seem to differ from other social living animals in that they form open societies, in the sense that conspecific individuals are freely exchangeable between colonies.

All authors theorizing on sociality in spiders (and other animals, except mixed species bird flocks and fish schools) have understood 'social' as something restricted to conspecifics (Wilson 1971; Vehrencamp 1979; Buskirk 1981). Social *Stegodyphus* spiders are believed to recognize conspecifics (Bradoo 1980). However, Kullmann et al. (1971, 1972) mixed newly hatched young of the permanently social *S. sarasinorum* with those of the periodically or "conditionally" (Millot and Bourgin 1942) social *S. lineatus* Latreille and kept this mixed

group for 3.5 months. This result is supported by the observation that young individuals of even solitary spiders allow contact with members of different species (Blanke 1972). The reactions of adult individuals therefore seemed more meaningful to investigate species recognition.

As the present study further shows, *Stegodyphus mimosarum* and *S. dumicola* colonies would be open even to members of the other species. The high degree of heterospecific groupings in the experimental situation indicates a considerable interspecific tolerance. Similarly, Krafft (1970, 1971) mixed the two social species *Agelena consociata* and *A. republicana* (for five days under observation) which suggests that species recognition might not be relevant in this situation. He did not mention the age class of his test animals, but all age classes co-occur in *Agelena* colonies, so interspecific tolerance may be present in adults.

Solitary spiders often live peacefully together as spiderlings and become cannibalistic later in their ontogeny. Neotenic retention of juvenile tolerance has therefore been assumed to be the first step toward communal behavior (Kullmann 1968; Buskirk 1981); it would not, however, account for interspecific tolerance. An interattraction of individuals could account for tolerance up to the point where competition would be counterselective. Under competition, selection (including kin-selection) can be expected to exclude xenogenetic individuals from tolerance. However, an individual's decision to attack or tolerate a stranger would still be governed by a cost/benefit ratio. For a socially living individual the cost factor may be most important: attacking will provoke defensive counteraggression, and the full risk of being severely damaged would fall upon the attacking individual, while costs arising from tolerance would be shared among all community members.

Mixed species *Stegodyphus* colonies are unknown from the field, perhaps because no one has looked for them. Both species co-occur closely in Transvaal, and the nearest interspecific colony distance that we encountered was 5 m within the same tree. On the other hand, our observations of the spiders suggest that the two *Stegodyphus* species would eventually separate according to their different behaviors (including walking speed, reaction times, etc.). *S. mimosarum* tends to live higher up in trees, while *S. dumicola* colonies are typically found closer to the ground (Seibt and Wickler 1988). Similarly in the genus *Agelena*, *A. consociata* prefers shadowy zones between lower bushes, while *A. republicana* builds its colonies in the crowns of trees exposed to the sun (Krafft 1970, 1971). Thus in both cases an ecological separation seems to counteract heterospecific groupings.

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THE EFFECT OF TEMPERATURE ON OVIPOSITION INTERVAL AND EARLY DEVELOPMENT IN *THERIDION RUFIPES* LUCAS (ARANEAE, THERIDIIDAE)

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ABSTRACT

The effect of temperature on oviposition rate and early development of *Theridion rufipes* in northern Queensland was investigated. Development did not proceed at 20°C, and embryos and postembryos responded differently to temperatures of 25°C and 30°C. The time interval between ovipositions by the female was markedly extended at 20°C, a temperature at which development was unlikely.

INTRODUCTION

Spider species for which the relationship between temperature and development has been reported include *Tegenaria atrica* (C. Koch) (Browning 1941), *Cheiracanthium inclusum* (Hentz) (Peck and Whitcomb 1970), *Thanatus striatus* (C. Koch) and *Allomengea scopigera* (Grube) (Schaefer 1977) and *Latrodectus hasselti* Thorell (Downes 1987). The present study adds *Theridion rufipes* Lucas to this list, and shows that the oviposition intervals (i.e., the time periods between the construction of egg sacs, over the iteroparous sequence) are temperature-dependent in a comparable way.

T. rufipes is widely distributed, primarily in tropical and subtropical regions, but with a range extending into temperate zones; it was first described from specimens collected in Algeria. Its original range may be hard to determine because its close association with man has probably led to extensive transportation. A recent first report (Sugarman 1979) of its occurrence in the Marshall Islands, for instance, may reflect its previous introduction by man. In the United States its range includes Texas and Florida (Levi and Randolph 1975).

MATERIALS AND METHODS

A total of 60 *T. rufipes* females was collected in Townsville, of which 51 were immature and unmated and nine were mature and had mated and produced their first egg sac in the field. These females were separated into three groups of 20 (17 immature, three mature in each case), and each group was kept at one of three experimental temperatures (20, 25 and 30°C \pm 1°C). The photoperiod was in

each case 14/10 hours light/dark. After their maturation molt, the previously immature females were mated, and on those (31) occasions when mating took place directly, and the male was either then killed by the female or removed, it was possible to record the time from mating to first oviposition. Times between subsequent ovipositions of all females (lab-mated and field-mated) were routinely recorded.

Spiders were confined individually in glass tubes measuring 50×20 mm diameter, with perforated plastic stoppers. Twice weekly, each was fed an identical diet of insect prey, including *Drosophila* sp., muscoid flies and native cockroaches. Water was not provided.

Observations were normally made daily; when ovipositions, hatchings, molts or emergences coincided with missed daily inspections, these data were not included in the results. Hence, although the spiders produced 338 egg sacs, only 287 of these gave oviposition interval values and 249 provided development data at 25 and 30°C; those (45) sacs that were constructed at 20°C gave the negative results for development at that temperature. All sacs were incubated at the same temperatures at which they were constructed.

Embryonic development times were obtained from 60 egg sacs which were teased open and housed in glass cavity blocks, the glass covers of which were separated from the rims of the blocks by a layer of non-absorbent cotton wool, with a little vaseline as adherent. By pseudoreplication, 40 of these same sacs gave postembryonic development times. The time from first molt to emergence was obtained from 189 egg sacs which were transferred to fresh 50×20 mm glass tubes with perforated plastic stoppers (these containers were also used for the 20°C sacs mentioned above), and kept intact until emergence occurred. The interval between the first molt and emergence was calculated by subtraction of the oviposition-first molt time (as determined from teased-open sacs) from the oviposition-emergence time of the intact sacs. Some possible inaccuracies of this procedure were considered by Downes (1987).

All developmental data are for whole broods (i.e., egg sacs) rather than for individual spiderlings. Although individuals varied in their rate of development, developmental synchrony was very close at the temperatures at which development occurred in this study. The values for the interval between oviposition and emergence of spiderlings from the egg sac were necessarily whole-brood values, so it was felt justifiable to use whole-brood means to compute corresponding values for intervals between oviposition and hatching (= embryo) and between hatching and the first molt (= postembryo). Hatch time was defined as the time of the rupture of the chorion. Field temperatures were provided by the Geography Department of James Cook University.

RESULTS

Development did not proceed at 20°C. The mean duration, at 25 and 30°C, of the embryonic, postembryonic and first instar stages within the egg sac (i.e., from oviposition to hatching, molting and emergence respectively) are given in Table 1. The temperature increase of 5°C from 25°C produced a decrease in development time of 2.7 days (28%) for the embryonic stage but only 0.3 days (14%) for the postembryonic stage.

Table 1.—The early development of *Theridion rufipes*. Values are given as mean interval in days, with standard error and (sample size). Cumulative values (cumul.) are given as values only. Values are means of whole broods (i.e., egg sacs), not of individual spiderlings.

| Developmental stage | Duration of Developmental Stages | | | | |
|---------------------------|----------------------------------|-------------------|--------|------------------|--------|
| | 20°C | 25°C | cumul. | 30°C | cumul. |
| Embryo | No devel. (45) | 9.8 SE 0.18 (45) | 9.8 | 7.1 SE 0.27 (15) | 7.1 |
| Postembryo | — | 2.1 SE 0.22 (27) | 11.9 | 1.8 SE 0.37 (13) | 8.9 |
| First instar to emergence | — | 2.4 SE 0.07 (124) | 14.3 | 3.2 SE 0.27 (65) | 12.1 |

Despite the fact that the overall development time from oviposition to emergence decreased by 2.2 days (15%) with the same temperature change (Table 1, cumulative values), the within-sac first instar stage time actually increased by 0.8 days (33%), from 2.4 to 3.2 days (Table 1, non-cumulative values).

There was no evidence that the adult female spiders were adversely affected by the experimental temperature extremes of 20 and 30°C, except that matings were rarer at the former temperature. However, the oviposition sequence was significantly extended at 20°C. Times, in days, separating the ovipositions of the iteroparous sequence are presented in Table 2. It is unfortunate that so few (three) instances were recorded of mating-oviposition at 20°C because the mean of these few values is by far the highest of those presented. The time between mating and the first oviposition is much shorter than that between subsequent ovipositions at temperatures that favor normal early development, but the data of Table 2 suggest that the reverse may be true at a temperature at which development is not assured.

DISCUSSION

As in all poikilotherms, temperature is usually the most critical environmental factor influencing the rate of development. However, an animal rarely develops under a constant unchanging temperature regime but rather experiences daily temperature variation around a gradually changing seasonal mean. *Latrodectus hasselti*, for example, commonly experiences temperatures of 30°C or greater in Townsville, but 30°C is close to an upper limit of temperature tolerance if applied continuously (Downes 1987).

The relative duration of the three pre-emergence phases of *T. rufipes* (embryo, postembryo and the first instar (part)) alters with the temperature change. The embryonic period takes up 69% of the total time to emergence at 25°C but only 59% of the total time at 30°C. The relative duration of the much shorter

Table 2.—The effect of temperature on time from mating to first oviposition and between subsequent ovipositions in *Theridion rufipes*. Values are given as mean interval in days, with standard error and (sample size).

| Temperature (°C) | Mating to first oviposition | Subsequent oviposition intervals |
|------------------|-----------------------------|----------------------------------|
| 20 | 47.7 SE 0.37 (3) | 26.2 SE 2.16 (38) |
| 25 | 6.6 SE 1.03 (17) | 16.1 SE 0.57 (123) |
| 30 | 6.3 SE 1.08 (11) | 14.1 SE 0.61 (95) |

postembryonic period remains unaltered (15% of the total time), while the relative (and indeed the absolute) time from the first ecdysis to emergence increases from 17% at 25°C to 26% at 30°C. This does not in itself imply any difference in the physiological response to temperature between embryos and postembryos, or between embryos and first instar spiderlings; it may be that the first instar spiderlings respond to high temperatures by remaining in the egg sac. This would be advantageous because the spiderlings would desiccate more rapidly once out of the cocoon owing to their increased exposure and increased activity. If this is so, moderately high temperatures may prolong the time spent in the egg sac by the first instars; this would explain the apparent increase in development time of the first instars in Table 1. In fact this phase is not a developmental stage in the same sense as the two earlier stages; the period from first to second ecdysis, rather than that from first ecdysis to emergence, would be more comparable.

It is not clear why the embryo and postembryo stages respond differently to a temperature decrease of 5°C from 30°C, the embryo stage increasing its development time by 38% (2.7 days) and the postembryo stage by only 17% (0.3 days). These differences may relate to the (unknown) overwintering strategy of this species in temperate zones. A 'stronger' response from embryos than from postembryos suggests physiological affinities with populations that undergo egg overwintering, but most spider species do not overwinter in the egg stage, according to Foelix (1982).

In temperate regions *T. rufipes* may be found to develop (slower) at temperatures down to 10°C or below, as does *Latrodectus hasselti* from temperate zones (Forster 1984). Why this does not occur in tropical populations is an open question, but over the past six years the mean monthly temperature in this district of Townsville has fallen below 19°C only in one two-month period, when it sank to 18.3°C (June and July 1982). Minimum temperatures do occasionally go below 10°C during some nights of the cooler dry season, but corresponding day temperatures on these occasions are likely to be in excess of 20°C.

A temperature cycle of 15-25°C, evenly changing over a 24-hour period, may produce a very different outcome from a constant 20°C regime, despite the former's mean value of 20°C.

In view of the curtailment of development at 20°C, the data of Table 2 suggest that there may be a behavioral response on the part of *T. rufipes* females, delaying the production of egg sacs at temperatures at which development is unlikely. In a poikilotherm such as *T. rufipes* physiological processes such as oögenesis will be subject to the effects of temperature just as surely as will embryonic development, but it would be interesting if it could be demonstrated that oviposition behavior responds more strongly than physiological/metabolic processes, to a fall in temperature of 5°C from 25 to 20°C. Such an investigation was beyond the scope of the present study.

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THE SPIDER GENUS *PARATHEUMA* BRYANT (ARANEAE, DESIDAE)

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ABSTRACT

The genus *Swainsia* Marples, 1964, is newly synonymized with *Paratheuma* Bryant, 1940. The previously unknown male of *P. insulana* (Banks) and female of *P. armata* (Marples) are described and illustrated. Habitat data and new distribution records are provided for these two species. The family Desidae is reported from the United States for the first time.

INTRODUCTION

Members of the genus *Paratheuma* are rare and poorly known spiders. The primary literature on them is limited to six papers (Banks 1902, 1903; Bryant 1940; Marples 1964; Roth and Brown 1975; Platnick 1977); the total number of specimens reported is only 19, although Roth and Brown (1975) apparently did not list all the specimens they collected, and Banks (1903) gave no data on number of specimens. This apparent rarity is no doubt a result of the restricted littoral and intertidal habitat of the spiders. Where found, they may be reasonably common, as indicated by the records presented below.

Only two species have hitherto been recognized as belonging to the genus (Platnick 1977): *Eutichurus insulanus* Banks, 1902, from Cuba, Haiti and Bermuda; and *Corteza interaesta* Roth and Brown, 1975, from the Gulf of California. To these may now be added a third species, *Swainsia armata* Marples, 1964, from Swains Island, American Samoa.

It is remarkable that these three congeneric species have been described not only in separate genera, but in separate families—*Eutichurus insulanus* in the Clubionidae (later transferred to the Gnaphosidae), *Corteza* in the Desidae, and *Swainsia* in the Agelenidae. It is quickly evident from the species' morphology that the only classical family in which they could be placed is the family Agelenidae. Their assignment to the Clubionidae and Gnaphosidae can be

regarded only as a blunder, even by the standards of the time, resulting from careless observation. The family Desidae, in which the genus is now placed, has received widespread acceptance only recently. Bryant (1940) established the genus *Paratheuma* for *E. insulanus* and *P. isolata*, incorrectly placing the genus in the Gnaphosidae, and including erroneous observations in the generic description. *Paratheuma isolata* has been transferred to the genus *Syrisca* (Clubionidae).

Genus *Paratheuma* Bryant

Paratheuma Bryant 1940:387, type species by original designation *Eutichurus insulanus* Banks. Roewer 1954:353. Platnick 1977:199.

Swainsia Marples 1964:403, type species by monotypy *Swainsia armata* Marples. Brignoli 1983:52. NEW SYNONYMY.

Corteza Roth and Brown 1975:2, type species by original designation and monotypy *Corteza interaesta* Roth and Brown. First synonymized with *Paratheuma* by Platnick 1977:199.

Description.—Color in life. Chelicerae orange brown to dark brown. Endites, labium and cephalic portion of carapace orange brown to brown, thoracic portion of carapace lighter. Sternum yellow orange to orange brown. Legs yellow to gray. Abdomen grayish yellow to greenish gray, often with small yellowish flecks or indistinct chevrons flanking cardiac region in posterior 2/3 of dorsum. Carapace may have dusky patches or lines along intercoxal grooves. In alcohol color may fade so that abdomen and legs are nearly uniform pale yellow, carapace yellow brown.

Total length of females 3.2-5.9 mm, males 3.1-5.2 mm. Carapace length females 1.35-2.50 mm, males 1.50-2.72 mm. Carapace width (maximum) females 1.00-2.00 mm, males 1.05-2.04 mm. Carapace low, cephalic region not much higher than thoracic, and sloping gradually posteriad. Cephalic region width about 2/3 of maximum carapace width or slightly less. Eye rows virtually straight, or with anterior row slightly procurved. Eyes subequal in size, AME slightly smaller than others. Width of posterior eye row about 70% of head width, anterior row slightly narrower. AME dark, others light.

Chelicerae stout, somewhat geniculate at base, divergent distally. Male chelicerae somewhat porrect and more divergent than in females. Cheliceral surface mostly clothed with abundant short setae (shorter in males) with setal bases somewhat enlarged. Promarginal cheliceral teeth in proximal half of fang groove only, two large teeth and one smaller. Retromarginal teeth extending full length of groove, 5-8 small teeth, largest tooth distal.

Endites rectangular, about 1.5 times as long as wide, bluntly pointed distally, with conspicuous scopula of medially curving hairs. Labium short and broad, rounded to slightly emarginate distally. Sternum slightly longer than broad to as broad as long, truncate, extending to posterior edge of coxae 4, narrowed and rounded posteriorly. Hind coxae separated by width of one coxa or slightly less.

Legs slender. Femoral lengths of all legs shorter than to as long as carapace length in females, shorter to slightly longer in males. Leg length formula 4-1-2-3. Leg spines few, weak.

Male palp slender, cymbium only slightly wider than distal width of tibia. Cymbium narrowed, finger-like distally, bulb occupying less than to more than half its length. Palp relatively simple, embolus and conductor chief parts visible in ventral view. Embolus slender, originating near middle of medial edge of bulb, or

somewhat more basally, curving forward to alveolar margin and back to form almost complete circle, ending on pointed conductor, which extends proximally to overlap tibia. Tibia with short to long disto-medial apophysis, and sometimes short distolateral apophysis as well.

Abdomen oval, unmodified, thickly covered with short, fine, appressed hairs. Posterior spinnerets elongate, up to half length of abdomen, extending beyond abdominal tip 0.5-1.0 mm; 2-segmented, segments about equal in length. Anterior spinnerets 2-segmented, distal segment very short, separated basally by about width of spinneret. Median spinnerets shorter, 1-segmented. Colulus large, conspicuous, heavily setose (colulus mistaken for a "lobe of spiracle" by Bryant, 1940, who described the genus as lacking a colulus). Tracheal spiracle broad, occupying about as much of abdominal width as pair of anterior spinnerets, separated from colulus by distance about equal to length of colulus.

Epigynum consisting of two small to large depressions, long axes varying from transverse to nearly longitudinal, with either edges only or entire surfaces sclerotized. Openings obvious or indistinct, ducts and receptacles appearing as two short to long longitudinal dark areas near medial edges of the depressions. Internal structures relatively simple (Fig. 6, see also Figs. 2, 4 in Platnick 1977). Overall epigynal size smallest in *P. insulana*, largest in *P. armata*.

Diagnosis.—The extension of the tracheae into the thorax, the absence of tarsal scopulae, the presence of a single row of tarsal trichobothria, and the genital structure separate the genus from other littoral genera of the family.

Paratheuma insulana (Banks)

Figs. 1, 4, 7, 10

Eutichurus insulanus Banks 1902:270 (female holotype from the Bermuda Islands, lost). Bonnet 1956:1845.

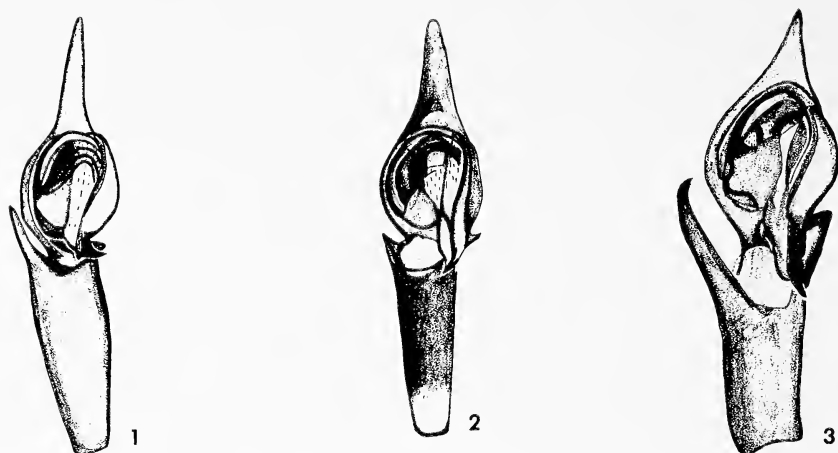
Paratheuma insulana (Banks), Bryant 1940:387; Roewer 1954:353; Platnick 1977:200.

Diagnosis.—The small size and oblique orientation of the epigynal depressions of the female, and the bifurcate, laterally projecting conductor tip of the male distinguish *P. insulana* from the other members of the genus.

Male.—Total length 3.5-5.0 mm, mean 3.86, SE 0.130. Carapace length 1.65-2.10 mm, mean 1.793, SE 0.039. Carapace width 1.15-1.55 mm, mean 1.290, SE 0.034 (ten specimens measured). Other measurements of one male: head width 0.85 mm, sternum length 1.0 mm, sternum width 1.0 mm, endite length 0.6 mm, labium length 0.35 mm, leg I—femur 1.75 mm, patella-tibia 2.25 mm, metatarsus-tarsus 2.45 mm, leg II—femur 1.75 mm, patella-tibia 2.1 mm, metatarsus-tarsus 2.4 mm, leg III—femur 1.55 mm, patella-tibia 1.9 mm, metatarsus-tarsus 2.35 mm, leg IV—femur 1.9 mm, patella-tibia 2.45 mm, metatarsus-tarsus 3.05 mm.

Bulb of palp smaller than that of other species, occupying less than 1/2 length of cymbium. Conductor bifurcate distally, with one branch extending laterally (Fig. 1).

Female.—Total length 3.3-5.9 mm, mean 4.32, SE 0.236. Carapace length 1.35-2.00 mm, mean 1.730, SE 0.058. Carapace width 1.00-1.45 mm, mean 1.238, SE 0.042 (ten specimens measured). Other measurements of one female: head width 0.9 mm, sternum length 0.95 mm, sternum width 0.9 mm, endite length 0.5 mm, labium length 0.35 mm, leg I—femur 1.55 mm, patella-tibia 2.0 mm, metatarsus-



Figs. 1-3.—Left pedipalps of male *Paratheuma* in ventral view: 1, *P. insulana* from Pigeon Key; 2, *P. interaesta* from Puerto Peñasco, Sonora, Mexico (holotype); 3, *P. armata* from Eniwetok, Marshall Islands.

tarsus 2.25 mm, leg II—femur 1.45 mm, patella-tibia 1.75 mm, metatarsus-tarsus 2.10 mm, leg III—femur 1.30 mm, patella-tibia 1.65 mm, metatarsus-tarsus 2.00 mm, leg IV—femur 1.70 mm, patella-tibia 2.20 mm, metatarsus-tarsus 2.75 mm.

Depressions of epigynum shorter and narrower than in other species, oriented obliquely. Internal genitalic structures are smaller than in others (Fig. 7).

Distribution.—Reported from Cuba (Bryant 1940), Haiti (Banks 1903), and the Bermudas (Banks 1902). Also known from the Florida Keys, Monroe Co., Florida, USA, Key Largo to West Summerland Key.

Habitat.—All specimens for which habitat data are available were collected among coral rubble (sometimes buried under plant detritus) above and below high water mark on sea beaches.

Material examined.—FLORIDA; *Monroe Co.*, Key Largo, 30 Dec. 1984, (J. W. Berry), 1 male, 2 females; Pigeon Key, 12 Mar. 1981, (J. W. Berry), 5 males, 5 females, 13 immatures, 25-28 Dec. 1984, (J. W. Berry), 1 male, 8 females, 63 immatures, 14 Mar. 1985, (J. W. Berry), 6 males, 7 females; Big Pine Key, 18 June 1965, 1 female, 5 immatures, in tidal litter, (W. Suter-FMNH), 28-29 Dec. 1984, (J. W. Berry), 1 female, 1 immature; West Summerland Key, 28 Dec. 1984, (J. W. Berry), 2 males.

Paratheuma interaesta (Roth and Brown)

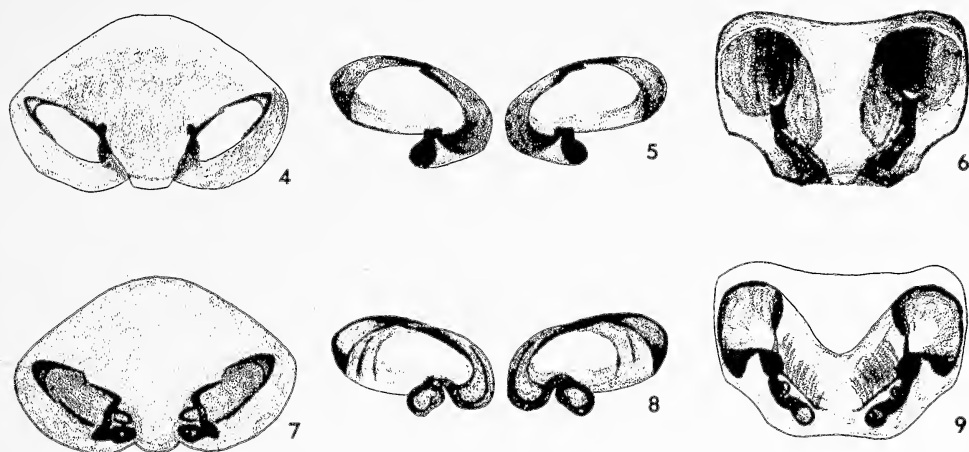
Figs. 2, 5, 8, 10

Corteza interaesta Roth and Brown 1975:3 (male holotype and female paratype from Pelican Point, Sonora, Mexico, in the American Museum of Natural History, examined).

Paratheuma interaesta: Platnick 1977:200.

Diagnosis.—The intermediate size of the genitalia of both sexes, transversely oriented main axis of the epigynal depressions of the female, and short tibial apophysis and simply pointed conductor of the male distinguish this species from the other two.

No additional information is available for this species, except for the collection of an immature specimen at the type locality, by Beatty, on 28 July 1962. The male palp and female epigynum are illustrated (Figs. 2, 5, 8) for comparison with the other species.



Figs. 4-9.—Epigyna of female *Paratheuma*: 4-6, ventral views; 7-9, dorsal views, cleared; 4, 7, *P. insulana* from Pigeon Key; 5, 8, *P. interaesta* from Puerto Peñasco, Sonora, Mexico (paratype); 6, 9, *P. armata* from Eniwetok.

Material examined.—MEXICO: SONORA; Norse Beach, Pelican Point, 27 March 1969, (V. Roth), 1 male, 1 female (holotype and paratype), 28 July 1962, (J. A. Beatty), 1 female, 1 immature.

Paratheuma armata (Marples), new combination

Figs. 3, 6, 9, 11

Swainsia armata Marples 1964:403 (male holotype from Swains Island, American Samoa, in Bishop Museum, Honolulu, examined). Brignoli 1983:521.

Diagnosis.—The relatively large epigynum of the female, which has large round depressions with the axis of depression plus ducts nearly longitudinal, and the very long medial and short lateral apophyses of the male palp clearly separate this species from *P. interaesta* and *P. insulana*.

Male.—Total length 3.1-3.8 mm, mean 3.45, SE 0.146. Carapace length 1.50-1.65 mm, mean 1.590, SE 0.026. Carapace width 1.05-1.25 mm, mean 1.180, SE 0.033 (five specimens measured). Other measurements of one male: head width 0.80 mm, sternum length 0.85 mm, sternum width 0.85 mm, endite length 0.50 mm, labium length 0.25 mm, leg I—femur 1.65 mm, patella-tibia 2.00 mm, metatarsus-tarsus 2.25 mm, leg II—femur 1.63 mm, patella-tibia 1.85 mm, metatarsus-tarsus 2.10 mm, leg III—femur 1.50 mm, patella-tibia 1.65 mm, metatarsus-tarsus 2.05 mm, leg IV—femur 1.75 mm, patella-tibia 2.10 mm, metatarsus-tarsus 2.60 mm.

Bulb of palp (Fig. 3) larger than in other species, occupying more than half length of cymbium and, when flexed, overlapping tibia by almost half length of cymbium; short, broad, collar-like lateral apophysis is present.

Female.—Total length 3.5-5.0 mm, mean 4.08, SE 0.198. Carapace length 1.50-1.90 mm, mean 1.658, SE 0.058. Carapace width 1.10-1.40 mm, mean 1.24, SE 0.048 (six specimens measured). Other measurements of one female: head width 1.05 mm, sternum length 1.0 mm, sternum width 0.95 mm, endite length 0.60 mm, labium length 0.35 mm, leg I—femur 1.70 mm, patella-tibia 2.15 mm, metatarsus-tarsus 2.30 mm, leg II—femur 1.65 mm, patella-tibia 2.00 mm,

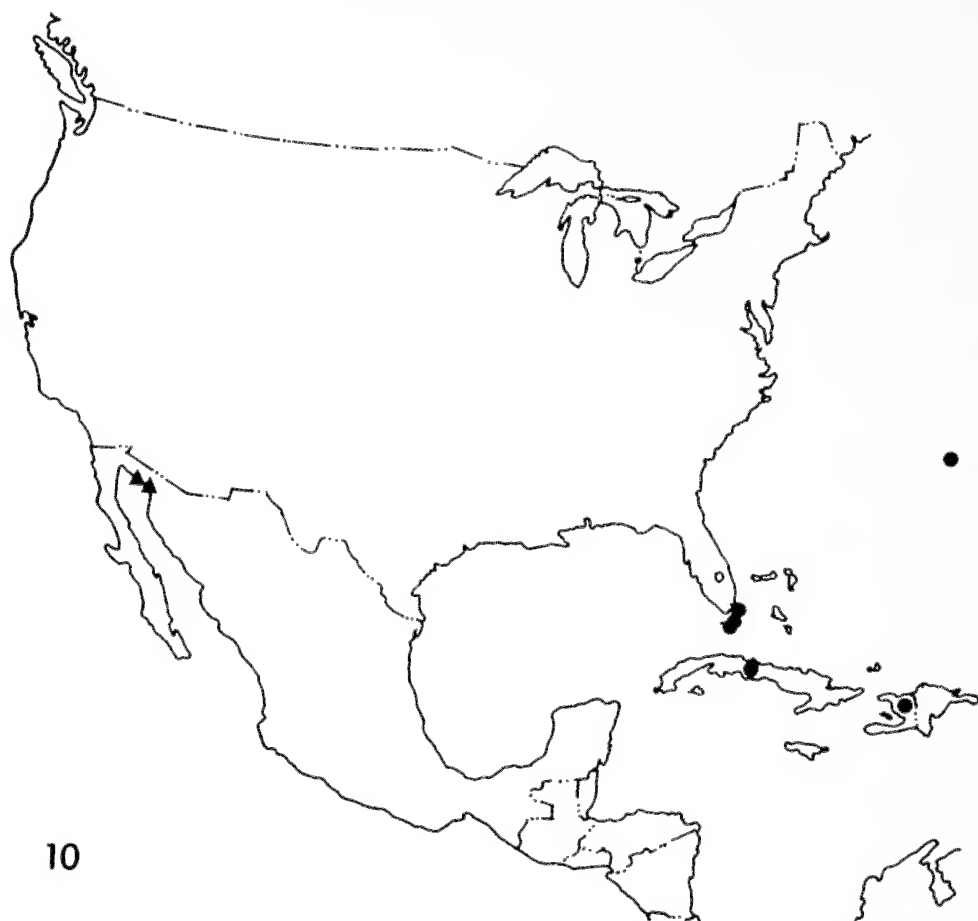


Fig. 10.—Distribution of *Paratheuma insulana* (circles) and *Paratheuma interaesta* (triangles).

metatarsus-tarsus 2.35 mm, leg III—femur 1.55 mm, patella-tibia 1.85 mm, metatarsus-tarsus 2.10 mm, leg IV—femur 1.90 mm, patella-tibia 2.35 mm, metatarsus-tarsus 2.75 mm.

Epigynum (Fig. 6) much larger than in other species, about 1 mm broad by $2/3$ mm long, occupying entire width of area between book lungs, and most of distance from base of pedicel to epigastric groove. Depressions broader, more widely separated than in other species; axis of depressions plus ducts almost parallel with midline. Entire depression, rather than edges only, sclerotized. Internal genitalic structures (Fig. 9) more extensive than in other species.

Distribution.—From American Samoa to the Marshall Islands and western Caroline Islands (Fig. 11).

Habitat.—All specimens for which data are available were taken among broken coral or other beach rubble near the upper edge of the drift line on sea beaches.

Material examined.—AMERICAN SAMOA: *Swains Island*, 20 Aug. 1940, (E. C. Zimmerman), 1 male (holotype, BISH). MARSHALL ISLANDS: *Eniwetok Atoll*, 9 June 1969, (J. W. Berry), 2 immature, 16 July 1968, (J. W. Berry and J. A. Beatty), 1 male, 1 female, 10 immature (SIU); *Kwajalein Atoll*, 8 Aug. 1969, (J. W. Berry), 6 immature (SIU); *Majuro Atoll*, 1 Aug. 1969, (J. W. Berry), 3 female, 12 immature, 31 July 1969, (J. W. Berry), 1 immature (SIU). CAROLINE ISLANDS: PALAU; *Kayangel Atoll*, 23 May 1973, (J. W. Berry and E. Berry), 1 male, 1 female, 3

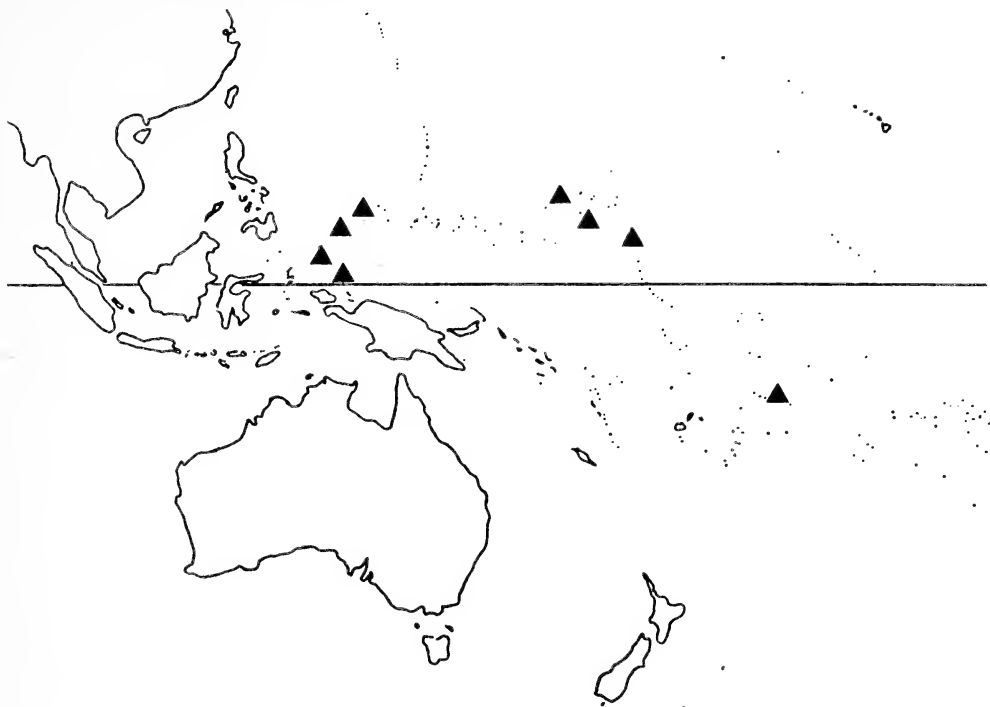


Fig. 11.—Distribution of *Paratheuma armata*.

immature (SIU); *Palau District*, Pulo Anna Isl., 7 Apr. 1973, (J. W. Berry and E. Berry), 1 male, 1 female, 6 immature (SIU), Sonsorol Isl., 10 Apr. 1973, (J. W. Berry and E. Berry), 1 male, 4 immature; YAP, 11 May 1980, (J. W. Berry), 1 male, 16 immature (SIU), *Ulihi Atoll*, 2 May 1980, (J. W. Berry and E. Berry), 1 male, 1 female (SIU).

DISCUSSION

The habitat, general appearance, and specific structures such as the genitalia, spinnerets, colulus, and tracheal system clearly place *Swainsia armata* with the other members of the genus *Paratheuma*. The taxonomic misplacement of *Paratheuma* undoubtedly was the primary reason for its being overlooked by the authors of the synonymous genera. Lack of definite locality or habitat data account for the rarity of *P. insulana* and *P. armata* in collections, as both are rather common to abundant in suitable habitats.

Although no specific collecting locality was given for the holotype of *P. insulana*, some information can be derived from the name of the collector, W. G. VanName, and the apparent date, May 1901. VanName was a specialist in tunicates and isopods, and collected at several specific localities in the Bermudas in May 1901. These localities are listed by him (VanName 1902) and, should it become desirable to restrict the type locality, one of them should probably be chosen.

Specimens of *P. insulana* and *P. armata* will be deposited in the collections of the American Museum of Natural History, New York, New York, the Museum of

Comparative Zoology, Cambridge, Massachusetts, and the Bishop Museum, Honolulu, Hawaii, (BISH). The remainder of the material will be kept in the Research Museum of the Department of Zoology, Southern Illinois University at Carbondale, Carbondale, Illinois, (SIU), and the Department of Biological Sciences, Butler University, Indianapolis, Indiana, (BU). The abbreviation FMNH was used for the Field Museum of Natural History.

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SPIDERS (ARANEAE) ASSOCIATED WITH STRIP-CLEARCUT AND DENSE SPRUCE-FIR FORESTS OF MAINE¹

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ABSTRACT

Spiders of 15 families, 76 genera, and at least 125 species were collected by pitfall traps in a spruce-budworm infested forest of northern Maine. Species of Lycosidae were numerically dominant and accounted for 56.2 and 54.1% of the total trapped specimens in 1977 and 1978, respectively. For both study years, significantly more ($P \leq 0.05$) individuals and species of spiders were captured in clearcut strips than in either uncut residual strips or dense stands. Peaks in seasonal activity of spiders generally coincided with the spruce budworm's early and late larval stages; spiders were also abundant and active during budworm oviposition and dispersal of 1st instars. Diversity of spider species was generally greater in dense stands and uncut residual strips than in clearcut strips. Individuals were distributed unevenly among species but more evenly in dense stands and uncut residual strips than in clearcut strips. Coefficients of community (CC) and percentage similarity (PS) values indicated more spider species than individuals were shared in common among forest conditions. Neither age of strip clearcut (1-6 years) nor litter depth had much influence on mean catches and mean numbers of species of spiders per trap per week.

INTRODUCTION

Spiders are among the dominant predators in many terrestrial communities (Gertsch 1979). In northeastern spruce-fir forests, arboreal spider densities are estimated to range from 187,500/ha (Morris 1963) to 312,500/ha (Haynes and

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Sisojevic 1966). These estimates do not include the epigeal and terricolous faunas that live near the ground. And, despite their common occurrence and potential importance as predators of insect pests (Riechert 1974), little is known about the species composition, diversity, and abundance of spiders that inhabit individual forest stands, forest-stand types, or forest communities in North America. Some earlier studies of forest-spider faunas include those of Dowdy (1950), Elliott (1930), Gibson (1947), Stratton et al. (1979), and Uetz (1979).

The possible adverse or beneficial effects of forest management practices on spider populations also have received scant attention, particularly in North America. Coyle (1981) studied the effects of clearcutting on the spider community of a southern Appalachian forest in North Carolina. The effects of silvicultural practices on European forest spiders have received more attention; studies include those by Huhta et al. (1967, 1969) and Huhta (1971).

As part of our investigations on natural enemies of the spruce budworm, *Choristoneura fumiferana* (Clem.), we studied the spider fauna of strip-clearcut and dense (uncut) spruce-fir forests of northern Maine in 1977 and 1978. Spruce budworms are susceptible to ground-inhabiting predators when 1st and 2nd instars disperse (Mott 1963; Jennings et al. 1983), and when large larvae and pupae drop from host-tree crowns to the forest floor (Morris and Mott 1963; Kelly and Régnière 1985). Our objectives were to: (1) determine the species of ground-inhabiting spiders in uncut residual strips, clearcut strips, and dense (uncut) spruce-fir stands, (2) determine seasonal activities of ground-inhabiting spiders as they relate to spruce budworm development, and (3) determine possible effects of strip clearcutting on species diversity and evenness of distribution of spiders. We also investigated effects of strip-clearcut age and litter depth on numbers and species of spiders.

MATERIALS AND METHODS

Study area.—We studied spiders in a dense spruce-fir forest infested with spruce budworm. Portions of the forest had been strip clearcut by mechanical harvesters; this created open strip areas with abundant shrubs and forbs, mainly *Rubus* spp. Strip clearcutting resulted in alternating clearcut and uncut residual strips (Fig. 1). Individual study sites were located from 48 to 61 km northwest of Millinocket, Piscataquis County, Maine, between Telos and Harrington Lakes (45° 45' to 46° 10' N, 68° 55' to 69° 20' W). Elevations ranged from about 360 to 425 m. The forest stands previously had been infested with spruce budworm for 4 to 5 years. The study area was sprayed with Sevin-4-oil® for spruce budworm suppression in 1976, but was not sprayed in 1977 or 1978. Budworm population estimates were 92.8 larvae-pupae/m² of balsam-fir foliage in 1977, and 100.7 larvae-pupae/m² of foliage in 1978.

Five strip-clearcut stands and five nearby dense (uncut) stands were investigated in 1977; seven strip-clearcut stands and three dense stands were investigated in 1978. In 1978, three each of the strip-clearcut and dense stands were the same as those studied in 1977; four additional strip-clearcut stands were investigated to obtain information on possible effects of strip-clearcut age on spider populations. Strip widths ranged from 23.4 to 49.7 m for uncut residual

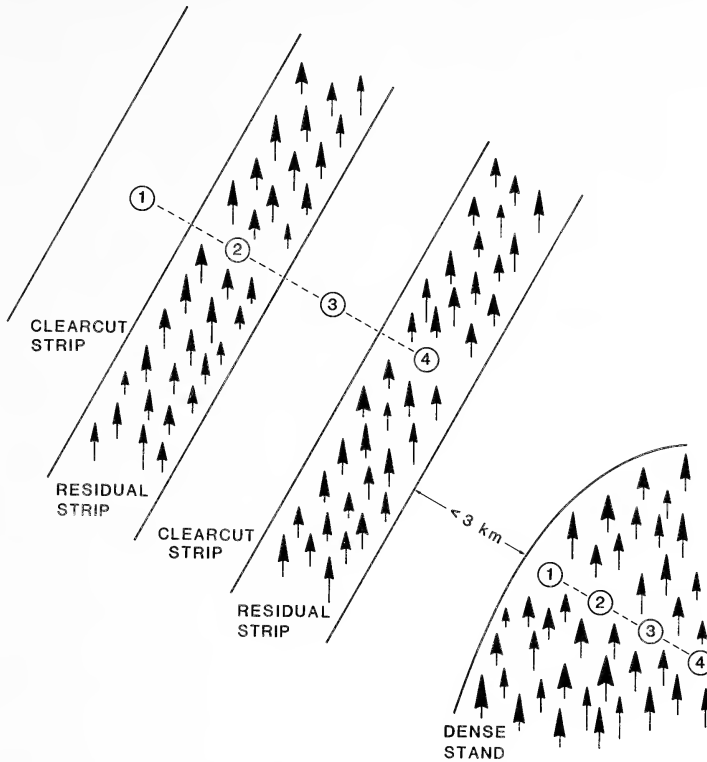


Fig. 1.—Pitfall-trap layout in strip-clearcut (uncut residual and clearcut strips) and in nearby dense (uncut) spruce-fir stands, Piscataquis County, Maine.

strips and from 19.1 to 29.7 m for clearcut strips investigated in 1977. Strip widths were not measured in 1978 but were comparable to those studied in 1977.

Mean basal areas, tree heights, and stand ages in 1977 were: 33.1 m²/ha, 17.3 m, and 73.7 years for uncut residual strips; 41.5 m²/ha, 15.4 m, and 73.5 years for dense stands. Most study sites had a predominantly softwood component of balsam fir, *Abies balsamea* (L.) Mill.; red spruce, *Picea rubens* Sargent; white spruce, *P. glauca* (Moench) Voss; black spruce, *P. mariana* (Miller) B.S.P.; northern white cedar, *Thuja occidentalis* L.; and white pine, *Pinus strobus* L. Common hardwood species were paper birch, *Betula papyrifera* Marshall; yellow birch, *B. alleghaniensis* Britton; and red maple, *Acer rubrum* L. Species composition by percentage basal area indicated that dense stands had more spruce (80%) than fir (11%), whereas spruce (45%) and fir (43%) were about equally represented in the uncut residual strips studied in 1977. The additional uncut residual strips studied in 1978 had more spruce (61%) than fir (30%). Hardwood basal area percentages generally were < 5% for both dense stands and uncut residual strips.

Understory vegetation differed markedly among the forest conditions. The open cleared strips had an abundance of flowering shrubs and forbs such as *Kalmia angustifolia* L., *Prunus pensylvanica* L., *Vaccinium angustifolium* Aiton, and *Rubus* spp. The uncut residual strips and dense stands, on the other hand, were characterized by few, widely spaced or clumped plants such as *Maianthemum canadense* Desfontaines, *Oxalis montana* Rafinesque-Schmaltz, and *Cornus canadensis* L. No quantitative plant data were taken; however, plants of 21

families, 43 genera, and at least 50 species were collected and identified (Jennings and Houseweart, unpublished data). Most plant species were collected in open areas of strip clearcuts; only five species were collected in uncut residual strips and 10 species in dense (uncut) stands.

Pitfall traps.—Forty large-capacity pitfall traps (Houseweart et al. 1979) were used each year for collecting spiders. Although pitfall catches are biased toward active forms, pitfall trapping remains the best available means for sampling wandering spiders (Uetz 1975), and trap catches give a closer estimate of species diversity than quadrat sampling (Uetz and Unzicker 1976). Our large-capacity trap (1 liter) had a 30-cm² apron with a 14.9-cm-diameter hole for funnel-bottle suspension. Cutler et al. (1975) showed that traps with aprons caught twice as many dionychous spiders compared to traps without aprons. We added ca. 300 ml of a 1:1 mixture of ethylene glycol and 70% ethanol to each trap bottle as a killing-preserved agent.

Four traps were placed in each strip-clearcut area, one each in two cut strips and in two adjacent uncut residual strips (Fig. 1). Correspondingly, four traps were placed in each nearby dense (uncut) stand investigated. Trap spacings in strip clearcuts were duplicated in dense stands. Traps were installed on 26 May and their contents collected weekly thereafter for 10 weeks from 2 June to 4 August 1977. In 1978, traps were installed on 18 May and contents collected weekly thereafter for 11 weeks from 25 May to 3 August. For both study years, trapping periods corresponded with spruce budworm activity, i.e., larval feeding in May and June; pupation in late June; moth emergence, mating, and egg laying in mid July (Houseweart et al. 1982); and dispersal of 1st instars in late July (Jennings et al. 1983).

Trap contents were sorted in the laboratory; all spiders were removed and stored in 2-dram neoprene-stoppered vials containing 70% ethanol. Species determinations were made chiefly after Kaston (1981). Other consulted sources included: Opell and Beatty (1976) for the hahniids; Leech (1972) for the amaurobiids; Chamberlin and Gertsch (1958) for the dictynids; Levi (1957) for species of *Theridion*; Dondale and Redner (1982) for the clubionids; Dondale and Redner (1978) for the philodromids and thomisids; and Kaston (1973) for species of *Metaphidippus*. Numerous taxonomic papers were consulted for identification of the erigonids; most were identified by comparison with published species descriptions and with voucher specimens housed in the Canadian National Collection, Ottawa. A few adult erigonids could not be determined to species and were designated as sp. 1, sp. 2, etc.

Because most species descriptions are based chiefly on the genitalia, only sexually mature spiders were identified to species. Juvenile and penultimate stages were identified to generic level; recently emerged spiderlings to family level. A few badly damaged specimens were undeterminable. Representative specimens of most collected spider species are deposited in the arachnid collections of the American Museum of Natural History, New York; the Canadian National Collections of Insects, Arachnids, and Nematodes, Ottawa; and, the U.S. National Museum of Natural History, Washington.

Litter depth.—Because litter structure and depth significantly affect abundances of some forest floor spiders (Uetz 1979; Bultman et al. 1982), we measured litter depth (cm) near each pitfall trap ($n = 40$). Measurements were summed and

means calculated over all replications by forest stand condition (uncut residual strip, clearcut strip, dense stand).

Data analysis.—Pitfall-catch data were subjected to Hartley's Test for homogeneity of variance prior to statistical analyses. Natural log transformations, $\ln(X + 1)$, were used to stabilize variances. Analysis of variance (ANOVA) and Duncan's Multiple Range Test were used to evaluate differences in pitfall catches over all weeks among the three forest stand conditions (uncut residual strips, clearcut strips, and dense stands) at $P \leq 0.05$. Regression analyses were used to evaluate the effects of strip-clearcut age (1-6 yr) and litter depth (independent variables) on mean catches of both individuals and species (dependent variables) per trap per week, where R^2 = coefficient of determination.

Because our pitfall collections represented finite populations where all captured individuals were counted and identified (Pielou 1966; Poole 1974), we used Brillouin's diversity formula to calculate species diversity. The formula as defined by Pielou (1975 p. 10) is: $H = 1/N \log N! / \prod N_i!$ where N is the number of individuals in the whole collection (i.e., for each forest condition) and N_i is the number in the i th species for $i = 1, \dots, s$. Brillouin's formula has been used to compare pitfall-catch diversities of spiders (Doane and Dondale 1979), carabid beetles (Reeves et al. 1983), phalangids (Jennings et al. 1984), and ants (Jennings et al. 1986). A measure of evenness was determined by the formula $J = H/H_{\max}$ where H is Brillouin's diversity and H_{\max} is the maximum possible diversity. Two measures of similarity among forest conditions were made using coefficient of community (CC) and percent similarity (PS) (Pielou 1975), where (CC) measures similarity between species lists and (PS) measures similarity between species quantities.

RESULTS

Numbers of individuals and species.—Fully 11,107 spiders, representing 15 families, 76 genera, and at least 125 species were collected by pitfall traps in spruce-fir forests of northern Maine. Fifteen families, 62 genera, and at least 97 species were trapped in 1977; 15 families, 66 genera, and at least 105 species were trapped in 1978 (Table 1). Generic and species composition differed between years. Ten species were captured in 1977 but not in 1978; 14 species were trapped in 1978 but not in 1977. For both years of trapping, individuals of Lycosidae were numerically dominant, comprising 56.2 and 54.1% of the total specimens trapped in 1977 and 1978, respectively. The Erigonidae, Amaurobiidae, and Agelenidae were next in abundance; each of the remaining families accounted for less than 10% of the total spiders caught either year.

Although the 40 pitfall traps were distributed unevenly among forest conditions, for both study years more spiders were captured in the clearcut strips than in either the uncut residual strips or in the dense spruce-fir stands. By far the majority of spiders caught in the open, cleared strips were species of *Pardosa* and undetermined lycosid spiderlings. Members of no other genus or family approached the abundance of wolf spiders in clearcut strips.

For both study years, about equal numbers of spider species were collected in dense, uncut spruce-fir stands (Table 1). In 1978, more species of spiders were caught in clearcut strips than the other two forest conditions.

Table 1.—Species and numbers of spiders collected in pitfall traps, three forest conditions, Telos Lake area, Piscataquis County, Maine, 1977-1978 (C = clearcut strips; R = uncut residual strips; D = dense stands; N = number of pitfall traps)

| | 1977 | | | | | 1978 | | | | |
|---------------------------------|------------------|------------------|------------------|-------|------|------------------|------------------|------------------|-------|------|
| | C | R | D | | | C | R | D | | |
| Spider Species | Strips (N=10) | Strips (N=10) | Stands (N=20) | Total | % | Strips (N=14) | Strips (N=14) | Stands (N=12) | Total | % |
| AGELENIDAE | | | | | | | | | | |
| <i>Agelenopsis utahana</i> | 1 | 3 | 4 | 8 | 0.20 | 22 | 23 | 11 | 56 | 0.79 |
| <i>Agelenopsis</i> sp. | 0 | 0 | 1 | 1 | 0.02 | 3 | 1 | 0 | 4 | 0.06 |
| <i>Cicurina brevis</i> | 7 | 9 | 17 | 33 | 0.83 | 10 | 26 | 24 | 60 | 0.85 |
| <i>Cicurina pallida</i> | 4 | 8 | 14 | 26 | 0.65 | 15 | 13 | 5 | 33 | 0.47 |
| <i>Cicurina placida</i> | 0 | 0 | 1 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Cicurina</i> sp. | 4 | 2 | 4 | 10 | 0.25 | 10 | 3 | 1 | 14 | 0.20 |
| <i>Coras montanus</i> | 0 | 0 | 4 | 4 | 0.10 | 1 | 1 | 1 | 3 | 0.04 |
| <i>Coras</i> sp. | 0 | 1 | 1 | 2 | 0.05 | 0 | 0 | 0 | 0 | |
| <i>Cryphoea montana</i> | 1 | 12 | 19 | 32 | 0.80 | 6 | 85 | 51 | 142 | 2.00 |
| <i>Cryphoea</i> sp. | 0 | 0 | 2 | 2 | 0.05 | 0 | 1 | 0 | 1 | 0.01 |
| <i>Wadotes calcaratus</i> | 5 | 43 | 105 | 153 | 3.81 | 33 | 121 | 102 | 256 | 3.61 |
| <i>Wadotes</i> sp. | 2 | 5 | 9 | 16 | 0.40 | 8 | 22 | 17 | 47 | 0.67 |
| HAHNIIDAE | | | | | | | | | | |
| <i>Antistea brunnea</i> | 1 | 0 | 1 | 2 | 0.05 | 0 | 0 | 1 | 1 | 0.01 |
| <i>Hahnina cinerea</i> | 0 | 0 | 5 | 5 | 0.12 | 2 | 0 | 2 | 4 | 0.06 |
| <i>Hahnina</i> sp. | 0 | 0 | 1 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Neoantistea agilis</i> | 0 | 0 | 0 | 0 | | 3 | 0 | 1 | 4 | 0.06 |
| <i>Neoantistea magna</i> | 69 | 14 | 16 | 99 | 2.46 | 256 | 65 | 33 | 354 | 5.00 |
| <i>Neoantistea</i> sp. | 8 | 0 | 1 | 9 | 0.22 | 52 | 1 | 2 | 55 | 0.78 |
| Undet. sp. | 1 | 0 | 2 | 3 | 0.08 | 1 | 0 | 0 | 1 | 0.01 |
| AMAUROBIIDAE | | | | | | | | | | |
| <i>Amaurobius borealis</i> | 8 | 42 | 134 | 184 | 4.58 | 33 | 42 | 18 | 93 | 1.32 |
| <i>Amaurobius</i> sp. | 2 | 0 | 2 | 4 | 0.10 | 0 | 0 | 0 | 0 | |
| <i>Callioplus euoplus</i> | 0 | 0 | 2 | 2 | 0.05 | 0 | 2 | 0 | 2 | 0.03 |
| <i>Callioplus tibialis</i> | 0 | 18 | 22 | 40 | 1.00 | 2 | 25 | 10 | 37 | 0.52 |
| <i>Callioplus</i> sp. | 1 | 0 | 0 | 1 | 0.02 | 0 | 2 | 1 | 3 | 0.04 |
| <i>Callobius bennetti</i> | 20 | 57 | 67 | 144 | 3.58 | 42 | 113 | 40 | 195 | 2.75 |
| <i>Callobius</i> sp. | 12 | 37 | 36 | 85 | 2.11 | 17 | 43 | 25 | 85 | 1.20 |
| Undet. sp. | 3 | 4 | 5 | 12 | 0.30 | 7 | 4 | 2 | 13 | 0.19 |
| DICTYNIDAE | | | | | | | | | | |
| <i>Dictyna brevitarsus</i> | 1 | 0 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Lathys pallida</i> | 0 | 0 | 2 | 2 | 0.05 | 0 | 0 | 1 | 1 | 0.01 |
| Undet. sp. | 0 | 1 | 2 | 3 | 0.08 | 0 | 0 | 1 | 1 | 0.01 |
| THERIDIIDAE | | | | | | | | | | |
| <i>Robertus fuscus</i> | 0 | 2 | 2 | 4 | 0.10 | 1 | 0 | 2 | 3 | 0.04 |
| <i>Robertus riparius</i> | 17 | 2 | 11 | 30 | 0.75 | 14 | 6 | 5 | 25 | 0.36 |
| <i>Robertus</i> sp. | 2 | 0 | 2 | 4 | 0.10 | 2 | 0 | 3 | 5 | 0.07 |
| <i>Theonoe stridula</i> | 0 | 0 | 11 | 11 | 0.28 | 0 | 2 | 10 | 12 | 0.17 |
| <i>Theridion montanum</i> | 0 | 0 | 0 | 0 | | 0 | 2 | 0 | 2 | 0.03 |
| <i>Theridion sexpunctatum</i> | 0 | 0 | 2 | 2 | 0.05 | 0 | 0 | 0 | 0 | |
| <i>Theridion</i> sp. | 0 | 0 | 2 | 2 | 0.05 | 0 | 0 | 2 | 2 | 0.03 |
| Undet. sp. | 1 | 0 | 1 | 2 | 0.05 | 0 | 0 | 0 | 0 | |
| LINYPHIIDAE | | | | | | | | | | |
| <i>Agyneta olivacea</i> | 0 | 0 | 0 | 0 | | 0 | 1 | 1 | 2 | 0.03 |
| <i>Aphileta misera</i> | 1 | 0 | 0 | 1 | 0.02 | 1 | 0 | 0 | 1 | 0.01 |
| <i>Bathypantes pallidus</i> | 7 | 19 | 4 | 30 | 0.75 | 30 | 54 | 17 | 101 | 1.43 |
| <i>Bathypantes</i> sp. | 1 | 0 | 1 | 2 | 0.05 | 0 | 0 | 0 | 0 | |
| <i>Centromerus denticulatus</i> | 0 | 0 | 6 | 6 | 0.15 | 0 | 0 | 7 | 7 | 0.10 |

| | | | | | | | | | | |
|--|----|----|----|-----|------|----|----|-----|-----|------|
| <i>Centromerus furcatus</i> | 4 | 11 | 16 | 31 | 0.78 | 4 | 8 | 7 | 19 | 0.27 |
| <i>Centromerus longibulbus</i> | 0 | 0 | 1 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Centromerus persolutus</i> | 2 | 0 | 2 | 4 | 0.10 | 4 | 4 | 0 | 8 | 0.11 |
| <i>Lepthyphantes alpinus</i> | 0 | 16 | 19 | 35 | 0.88 | 3 | 37 | 50 | 90 | 1.27 |
| <i>Lepthyphantes complicatus</i> | 0 | 0 | 1 | 1 | 0.02 | 0 | 5 | 2 | 7 | 0.10 |
| <i>Lepthyphantes intricatus</i> | 2 | 13 | 3 | 18 | 0.45 | 6 | 14 | 4 | 24 | 0.34 |
| <i>Lepthyphantes</i> sp. near <i>arboreus</i> | 0 | 0 | 1 | 1 | 0.02 | 0 | 0 | 1 | 1 | 0.01 |
| <i>Lepthyphantes turbatrix</i> | 0 | 0 | 0 | 0 | | 0 | 2 | 0 | 2 | 0.03 |
| <i>Lepthyphantes zebra</i> | 0 | 0 | 1 | 1 | 0.02 | 0 | 0 | 2 | 2 | 0.03 |
| <i>Lepthyphantes</i> sp. | 0 | 2 | 2 | 4 | 0.10 | 0 | 0 | 0 | 0 | |
| <i>Meioneta simplex</i> | 0 | 0 | 0 | 0 | | 4 | 0 | 0 | 4 | 0.06 |
| <i>Oreonetides flavescens</i> | 0 | 0 | 0 | 0 | | 1 | 0 | 0 | 1 | 0.01 |
| <i>Oreonetides recurvatus</i> | 1 | 0 | 0 | 1 | 0.02 | 2 | 1 | 0 | 3 | 0.04 |
| <i>Oreonetides rotundus</i> | 0 | 2 | 0 | 2 | 0.05 | 1 | 0 | 1 | 2 | 0.03 |
| <i>Oreonetides vaginatus</i> | 0 | 10 | 22 | 32 | 0.80 | 4 | 19 | 14 | 37 | 0.52 |
| <i>Oreonetides</i> sp. 1 | 0 | 0 | 0 | 0 | | 0 | 0 | 2 | 2 | 0.03 |
| <i>Oreonetides</i> sp. 2 | 2 | 1 | 1 | 4 | 0.10 | 3 | 11 | 2 | 16 | 0.23 |
| <i>Porrhomma</i> sp. | 1 | 1 | 0 | 2 | 0.05 | 0 | 1 | 1 | 2 | 0.03 |
| <i>Wubana drassoides</i> | 0 | 2 | 1 | 3 | 0.08 | 0 | 2 | 0 | 2 | 0.03 |
| Undet. sp. | 2 | 1 | 1 | 4 | 0.10 | 10 | 18 | 24 | 52 | 0.74 |
| ERIGONIDAE | | | | | | | | | | |
| <i>Baryphma longitarsum</i> | 1 | 0 | 0 | 1 | 0.02 | 3 | 0 | 0 | 3 | 0.04 |
| <i>Carorita limnaeus</i> | 0 | 0 | 0 | 0 | | 0 | 0 | 2 | 2 | 0.03 |
| <i>Ceraticelus atriceps</i> | 1 | 0 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Ceraticelus fissiceps</i> | 0 | 0 | 0 | 0 | | 1 | 0 | 0 | 1 | 0.01 |
| <i>Ceraticelus laetabilis</i> | 5 | 6 | 1 | 12 | 0.30 | 21 | 16 | 3 | 40 | 0.57 |
| <i>Ceraticelus minutus</i> | 2 | 0 | 0 | 2 | 0.05 | 5 | 0 | 0 | 5 | 0.07 |
| <i>Ceratinella brunnea</i> | 13 | 5 | 34 | 52 | 1.30 | 32 | 81 | 83 | 196 | 2.77 |
| <i>Ceratinella</i> sp. | 9 | 2 | 2 | 13 | 0.33 | 6 | 5 | 6 | 17 | 0.24 |
| <i>Ceratinopsis auriculata</i> | 0 | 0 | 0 | 0 | | 0 | 1 | 0 | 1 | 0.01 |
| <i>Dicymbium elongatum</i> | 0 | 0 | 0 | 0 | | 1 | 0 | 1 | 2 | 0.03 |
| <i>Diplocentria bidentata</i> | 8 | 29 | 15 | 52 | 1.30 | 26 | 42 | 28 | 96 | 1.36 |
| <i>Diplocentria rectangulata</i> | 0 | 0 | 2 | 2 | 0.05 | 0 | 0 | 1 | 1 | 0.01 |
| <i>Diplocephalus cuneatus</i> | 1 | 0 | 1 | 2 | 0.05 | 0 | 0 | 0 | 0 | |
| <i>Eperigone entomologica</i> | 0 | 0 | 0 | 0 | | 0 | 4 | 3 | 7 | 0.10 |
| <i>Eperigone maculata</i> | 9 | 1 | 0 | 10 | 0.25 | 10 | 5 | 3 | 18 | 0.25 |
| <i>Eperigone trilobata</i> | 67 | 3 | 0 | 70 | 1.74 | 83 | 5 | 0 | 88 | 1.24 |
| <i>Erigone atra</i> | 1 | 1 | 0 | 2 | 0.05 | 0 | 0 | 0 | 0 | |
| <i>Erigone</i> sp. 1 | 1 | 0 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Erigone</i> sp. 2 | 1 | 0 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Floricomus plumalis</i> | 3 | 0 | 3 | 6 | 0.15 | 9 | 1 | 3 | 13 | 0.19 |
| <i>Gnathonaroides pedale</i> | 0 | 0 | 0 | 0 | | 0 | 0 | 1 | 1 | 0.01 |
| <i>Gonatium crassipalpus</i> | 0 | 1 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Grammonota angusta</i> | 0 | 2 | 2 | 4 | 0.10 | 0 | 6 | 7 | 13 | 0.19 |
| <i>Grammonota gigas</i> | 0 | 0 | 0 | 0 | | 12 | 1 | 0 | 13 | 0.19 |
| <i>Grammonota</i> sp. | 0 | 0 | 1 | 1 | 0.02 | 4 | 2 | 3 | 9 | 0.13 |
| <i>Halorates</i> sp. | 0 | 1 | 4 | 5 | 0.12 | 0 | 0 | 2 | 2 | 0.03 |
| <i>Islandiana longisetosa</i> | 0 | 0 | 0 | 0 | | 0 | 1 | 0 | 1 | 0.01 |
| <i>Oedothorax trilobatus</i> | 2 | 0 | 0 | 2 | 0.05 | 1 | 0 | 0 | 1 | 0.01 |
| <i>Pocadicnemis americana</i> | 13 | 11 | 76 | 100 | 2.49 | 87 | 27 | 100 | 214 | 3.01 |
| <i>Sciastes truncatus</i> | 1 | 2 | 5 | 8 | 0.20 | 0 | 0 | 8 | 8 | 0.11 |
| <i>Scirionis tarsalis</i> | 4 | 0 | 0 | 4 | 0.10 | 3 | 0 | 0 | 3 | 0.04 |
| <i>Scotinotylus pallidus</i> | 0 | 0 | 0 | 0 | | 0 | 1 | 0 | 1 | 0.01 |
| <i>Sisicottus montanus</i> | 2 | 11 | 21 | 34 | 0.85 | 7 | 48 | 12 | 67 | 0.95 |
| <i>Sisicus apertus</i> | 0 | 0 | 1 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Sisicus penifusiferus</i> | 0 | 0 | 1 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Tapinocyba bicarinata</i> | 0 | 3 | 3 | 6 | 0.15 | 1 | 0 | 6 | 7 | 0.10 |

| | | | | | | | | | | |
|----------------------------------|------|-----|----|------|-------|------|-----|----|------|-------|
| <i>Tapinocyba minuta</i> | 0 | 1 | 1 | 2 | 0.05 | 7 | 6 | 1 | 14 | 0.20 |
| <i>Tapinocyba simplex</i> | 0 | 3 | 13 | 16 | 0.40 | 6 | 14 | 15 | 35 | 0.49 |
| <i>Tunagyna debilis</i> | 10 | 4 | 3 | 17 | 0.42 | 18 | 20 | 11 | 49 | 0.69 |
| <i>Walckenaeria atrotibialis</i> | 0 | 0 | 2 | 2 | 0.05 | 7 | 0 | 0 | 7 | 0.10 |
| <i>Walckenaeria castanea</i> | 0 | 3 | 5 | 8 | 0.20 | 0 | 1 | 0 | 1 | 0.01 |
| <i>Walckenaeria communis</i> | 0 | 0 | 0 | 0 | | 1 | 0 | 1 | 2 | 0.03 |
| <i>Walckenaeria directa</i> | 0 | 0 | 1 | 1 | 0.02 | 2 | 0 | 6 | 8 | 0.11 |
| <i>Walckenaeria exigua</i> | 14 | 7 | 16 | 37 | 0.92 | 8 | 7 | 11 | 26 | 0.37 |
| <i>Walckenaeria spiralis</i> | 1 | 0 | 0 | 1 | 0.02 | 4 | 0 | 0 | 4 | 0.06 |
| <i>Walckenaeria teres</i> | 0 | 1 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| Undet. sp. | 8 | 5 | 28 | 41 | 1.02 | 23 | 12 | 12 | 47 | 0.67 |
| ARANEIDAE | | | | | | | | | | |
| <i>Araneus nordmanni</i> | 0 | 0 | 0 | 0 | | 1 | 0 | 0 | 1 | 0.01 |
| Undet. sp. | 1 | 0 | 2 | 3 | 0.08 | 3 | 2 | 1 | 6 | 0.06 |
| MIMETIDAE | | | | | | | | | | |
| <i>Ero canionis</i> | 1 | 0 | 1 | 2 | 0.05 | 0 | 0 | 1 | 1 | 0.01 |
| <i>Ero</i> sp. | 1 | 0 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| LYCOSIDAE | | | | | | | | | | |
| <i>Alopecosa aculeata</i> | 6 | 0 | 0 | 6 | 0.15 | 11 | 1 | 1 | 13 | 0.19 |
| <i>Alopecosa</i> sp. | 0 | 0 | 4 | 4 | 0.10 | 0 | 0 | 0 | 0 | |
| <i>Arctosa raptor</i> | 1 | 0 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Hogna</i> sp. | 2 | 0 | 0 | 2 | 0.05 | 0 | 0 | 0 | 0 | |
| <i>Pardosa fuscula</i> | 0 | 0 | 0 | 0 | | 1 | 0 | 0 | 1 | 0.01 |
| <i>Pardosa hyperborea</i> | 3 | 1 | 5 | 9 | 0.22 | 22 | 0 | 3 | 25 | 0.36 |
| <i>Pardosa mackenziana</i> | 290 | 37 | 10 | 337 | 8.38 | 504 | 91 | 24 | 619 | 8.74 |
| <i>Pardosa maesta</i> | 145 | 1 | 1 | 147 | 3.66 | 332 | 2 | 0 | 334 | 4.71 |
| <i>Pardosa xerampelina</i> | 314 | 12 | 0 | 326 | 8.11 | 770 | 75 | 7 | 852 | 12.03 |
| <i>Pardosa</i> sp. | 93 | 3 | 5 | 101 | 2.51 | 166 | 8 | 3 | 178 | 2.51 |
| <i>Pirata cantralli</i> | 2 | 0 | 0 | 2 | 0.05 | 0 | 0 | 0 | 0 | |
| <i>Pirata insularis</i> | 6 | 0 | 9 | 15 | 0.37 | 7 | 0 | 4 | 11 | 0.16 |
| <i>Pirata minutus</i> | 9 | 0 | 1 | 10 | 0.25 | 25 | 0 | 0 | 25 | 0.36 |
| <i>Pirata montanus</i> | 0 | 0 | 0 | 0 | | 2 | 0 | 1 | 3 | 0.04 |
| <i>Pirata piraticus</i> | 4 | 1 | 0 | 5 | 0.12 | 1 | 0 | 0 | 1 | 0.01 |
| <i>Pirata</i> sp. | 1 | 0 | 2 | 3 | 0.08 | 3 | 0 | 3 | 6 | 0.09 |
| <i>Trochosa terricola</i> | 6 | 2 | 34 | 42 | 1.05 | 37 | 21 | 53 | 111 | 1.57 |
| <i>Trochosa</i> sp. | 0 | 0 | 0 | 0 | | 5 | 3 | 3 | 11 | 0.16 |
| Undet. sp. | 1133 | 113 | 2 | 1248 | 31.04 | 1368 | 222 | 56 | 1646 | 23.23 |
| GNAPHOSIDAE | | | | | | | | | | |
| <i>Gnaphosa parvula</i> | 2 | 0 | 0 | 2 | 0.05 | 7 | 0 | 0 | 7 | 0.10 |
| <i>Gnaphosa</i> sp. | 0 | 0 | 0 | 0 | | 1 | 0 | 0 | 1 | 0.01 |
| <i>Haplodrassus signifler</i> | 1 | 0 | 0 | 1 | 0.02 | 2 | 0 | 1 | 3 | 0.04 |
| <i>Micaria pulicaria</i> | 0 | 2 | 0 | 2 | 0.05 | 1 | 0 | 0 | 1 | 0.01 |
| <i>Orodassus canadensis</i> | 0 | 1 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Zelotes fratris</i> | 9 | 0 | 2 | 11 | 0.28 | 27 | 0 | 2 | 29 | 0.41 |
| <i>Zelotes</i> sp. | 2 | 0 | 0 | 2 | 0.05 | 18 | 1 | 0 | 19 | 0.27 |
| Undet. sp. | 1 | 0 | 0 | 1 | 0.02 | 1 | 0 | 0 | 1 | 0.01 |
| CLUBIONIDAE | | | | | | | | | | |
| <i>Agroeca ornata</i> | 0 | 1 | 8 | 9 | 0.22 | 1 | 6 | 11 | 18 | 0.25 |
| <i>Agroeca</i> sp. | 0 | 0 | 2 | 2 | 0.05 | 0 | 0 | 1 | 1 | 0.01 |
| <i>Clubiona bishopi</i> | 1 | 0 | 0 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| <i>Clubiona canadensis</i> | 0 | 5 | 8 | 13 | 0.33 | 0 | 8 | 2 | 10 | 0.14 |
| <i>Clubiona</i> sp. | 3 | 0 | 1 | 4 | 0.10 | 0 | 7 | 2 | 9 | 0.13 |
| PHILODROMIDAE | | | | | | | | | | |
| <i>Philodromus placidus</i> | 1 | 1 | 1 | 3 | 0.08 | 1 | 2 | 1 | 4 | 0.06 |
| <i>Philodromus</i> sp. | 0 | 0 | 0 | 0 | | 0 | 1 | 1 | 2 | 0.03 |
| <i>Tibellus oblongus</i> | 0 | 0 | 0 | 0 | | 1 | 0 | 0 | 1 | 0.01 |
| THOMISIDAE | | | | | | | | | | |
| <i>Ozyptila distans</i> | 0 | 0 | 0 | 0 | | 0 | 0 | 1 | 1 | 0.01 |
| <i>Xysticus canadensis</i> | 0 | 19 | 35 | 54 | 1.34 | 2 | 88 | 95 | 185 | 2.61 |

| | | | | | | | | | | |
|---------------------------------|------|-----|-----|------|------|------|------|------|------|------|
| <i>Xysticus discursans</i> | 0 | 0 | 0 | 0 | | 1 | 0 | 0 | 1 | 0.01 |
| <i>Xysticus emertoni</i> | 0 | 0 | 0 | 0 | | 7 | 0 | 0 | 7 | 0.10 |
| <i>Xysticus</i> sp. | 0 | 0 | 2 | 2 | 0.05 | 0 | 2 | 2 | 4 | 0.06 |
| SALTICIDAE | | | | | | | | | | |
| <i>Euophrys cruciatus</i> | 4 | 0 | 1 | 5 | 0.12 | 0 | 0 | 0 | 0 | |
| <i>Evarcha hoyi</i> | 0 | 0 | 0 | 0 | | 2 | 0 | 0 | 2 | 0.03 |
| <i>Metaphidippus flavipedes</i> | 0 | 0 | 1 | 1 | 0.02 | 0 | 1 | 2 | 3 | 0.04 |
| <i>Pellenes montanus</i> | 0 | 0 | 0 | 0 | | 4 | 0 | 0 | 4 | 0.06 |
| <i>Phidippus borealis</i> | 0 | 0 | 0 | 0 | | 3 | 0 | 0 | 3 | 0.04 |
| <i>Phidippus whitmanii</i> | 0 | 0 | 0 | 0 | | 1 | 0 | 0 | 1 | 0.01 |
| <i>Sitticus finschii</i> | 0 | 0 | 1 | 1 | 0.02 | 0 | 0 | 0 | 0 | |
| Undet. sp. | 0 | 0 | 0 | 0 | | 0 | 0 | 1 | 1 | 0.01 |
| UNIDENTIFIABLE | 0 | 0 | 0 | 0 | | 1 | 0 | 0 | 1 | 0.01 |
| Subtotals: | | | | | | | | | | |
| Species | 59 | 51 | 68 | | | 76 | 56 | 69 | | |
| Individuals | 2412 | 639 | 971 | 4022 | | 4340 | 1627 | 1118 | 7085 | |

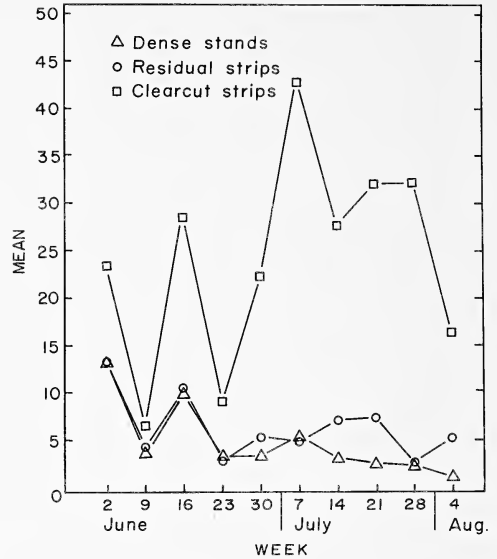
Species of spiders that showed habitat affinities both study years were: *Neoantistea magna* (Keyserling), *Eperigone trilobata* (Emerton), *Pardosa mackenziana* (Keyserling), *P. moesta* Banks, *P. xerampelina* (Keyserling), *Pirata minutus* Emerton, and *Zelotes fratris* Chamberlin for clearcut strips; *Bathypantes pallidus* (Banks) and *Diplocentria bidentata* (Emerton) for uncut residual strips; *Wadotes calcaratus* (Keyserling), *Callobius bennetti* (Blackwall), *Lepthyphantes alpinus* (Emerton), *Oreonetides vaginatus* (Thorell), *Ceratinella brunnea* Emerton, *Sisicottus montanus* (Emerton), and *Xysticus canadensis* Gertsch for uncut residual strips, dense stands, or both uncut forest conditions. Habitat preferences of *Pocadicnemis americana* Millidge and *Trochosa terricola* Thorell were undeterminable from our data. In 1977 and 1978, both species were most abundant in dense stands; however, in 1978, both species were also prevalent in clearcut strips. Pitfall catches for the remaining species showed no clear habitat preference or affinity.

Mean numbers of individuals and species.—For both study years, significantly more individuals (ANOVA, $F = 84.7$, $P \leq 0.0001$, 1977; $F = 41.7$, $P \leq 0.0001$, 1978) and more species (ANOVA, $F = 32.3$, $P \leq 0.0001$, 1977; $F = 13.4$, $P \leq 0.0001$, 1978) of spiders were captured in clearcut strips than in either uncut residual strips or dense stands (Table 2). And, for both study years, the most similar habitats (i.e., uncut residual strips and dense stands) did not differ significantly for mean numbers of individuals per trap per week. Likewise, mean numbers of species did not differ significantly either study year.

Table 2.—Mean numbers of individuals and spider species per trap per week by forest condition. Column means followed by the same letter are not significantly different at the $P \leq 0.05$ level, Duncan's multiple range test. Natural log transformations, $\ln(x + 1)$, were used to stabilize variances of mean numbers of individuals.

| Forest condition | $\bar{X} (\pm \text{SE})$ individuals | | $\bar{X} (\pm \text{SE})$ species | |
|------------------|---------------------------------------|---------------|-----------------------------------|--------------|
| | 1977 | 1978 | 1977 | 1978 |
| Clearcut strips | 24.12a (2.21) | 28.18a (2.04) | 5.98a (0.27) | 7.40a (0.35) |
| Residual strips | 6.39b (0.70) | 10.56b (0.80) | 3.94b (0.29) | 5.77b (0.31) |
| Dense stands | 4.85b (0.33) | 8.48b (0.64) | 3.33b (0.19) | 5.06b (0.32) |

Fig. 2.—Mean catches of spiders per trap per week; week 1 = 2 June 1977. Open triangles = dense spruce-fir stands; open circles = uncut residual strips; open squares = clearcut strips.



Seasonal activity.—Spiders were active during most of the spruce budworm's developmental stages; however, seasonal activities varied between study years and among forest conditions (Figs. 2 and 3). For both study years, mean catch densities per week were greater in clearcut strips; whereas, mean catches were about equal for uncut residual strips and dense stands. In both 1977 and 1978, peak catches were observed the 3rd and 6th weeks for clearcut strips; the latter peaks generally corresponded with emergence of young spiderlings. Mean catches of individuals per week generally declined about the 3rd (1977) and 2nd (1978) weeks of trapping for both dense stands and uncut residual strips.

Mean species per trap also fluctuated between years and among forest conditions (Figs. 4 and 5). Strip clearcuts generally had more species per trap per week than the other two forest conditions. For both study years, mean species catch rate generally declined after the 5th and 6th weeks of trapping; however, in 1978 catch rates increased during the 10th and 11th weeks.

Species diversity and evenness.—Although more individuals and species of spiders were captured in clearcut strips, species diversity and evenness of pitfall-trap catches were generally greater in dense stands and uncut residual strips (Table 3). The most similar habitats (i.e., uncut residual strips and dense stands) had comparable diversity and evenness values both years. No doubt the uneven distribution of individuals in clearcut strips contributed to lower species diversity for these habitats. Species diversity increases as individuals become more evenly distributed (Price 1975). The higher observed variances in mean individuals per trap per week (Table 2) also indicate unevenly distributed individuals for clearcut-strip habitats.

Coefficient of community and percentage similarity.—Strip-clearcut areas (uncut residual and clearcut strips) and dense stands shared about the same number of species of spiders either study year; CC = 68.1 in 1977; CC = 66.2 in 1978. Surprisingly, the most dissimilar neighboring habitats (i.e., uncut residual and clearcut strips) had only slightly fewer species in common; CC = 58.7 in 1977; CC = 62.1 in 1978.

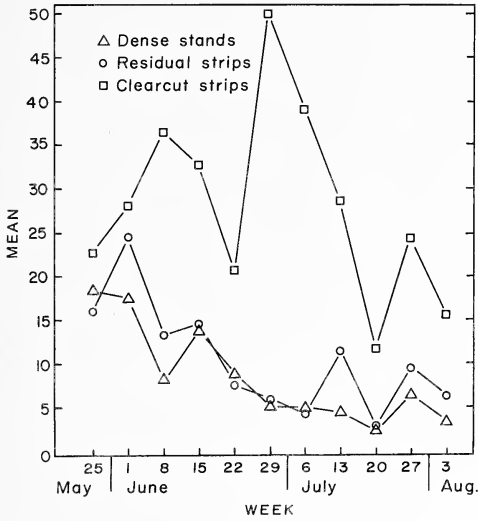


Fig. 3.—Mean catches of spiders per trap per week; week 1 = 25 May 1978. Open triangles = dense spruce-fir stands; open circles = uncut residual strips; open squares = clearcut strips.

Among strip-clearcut areas and dense stands, percentage similarity in numbers of individuals of each spider species was about the same both study years, i.e., $PS = 39.6$ in 1977; $PS = 39.9$ in 1978. However, comparing catches *within* strip clearcuts (uncut residual vs. clearcut strips) showed that fewer individuals shared these habitats in common in 1977 ($PS = 22.8$) than in 1978 ($PS = 32.8$). The relatively low PS values support our hypothesis that the unevenly distributed individuals in clearcut strips contributed greatly to lower species diversity for these habitats.

Age of strip clearcut.—Regression analyses indicated that age of strip clearcut (1-6 years) had little influence on mean catches of individuals ($R^2 = 0.08$, $P > 0.37$) and mean numbers of species ($R^2 = 0.41$, $P > 0.02$) of spiders/trap/week.

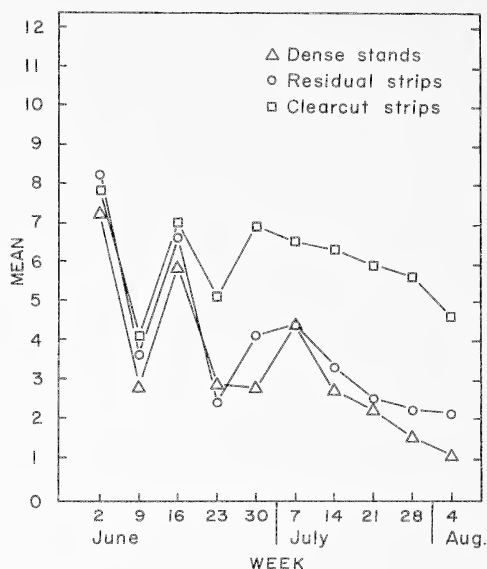
Litter depth.—Mean litter depth was significantly greater ($P \leq 0.01$) in dense stands ($\bar{X} = 11.7$ cm) than in either uncut residual ($\bar{X} = 8.5$ cm) or in clearcut strips ($\bar{X} = 8.0$ cm). Uncut residual and clearcut-strip means did not differ significantly. Regression analyses indicated that litter depth had little influence on either mean catches ($R^2 = 0.04$, $P \geq 0.08$) or mean species ($R^2 = 0.05$, $P \geq 0.05$) of spiders/trap/week.

DISCUSSION

Few previous studies have dealt with Maine spiders. The spider fauna of Mount Desert Island, Hancock County, has been studied most extensively; Procter (1946) listed 15 families, 94 genera, and 179 species from various habitats on the island. Earlier, Bishop and Clarke (1923) reported spiders of 10 families, 23 genera, and 29 species from Isle au Haut, Knox County, Maine. Blake (1926) studied the biota of Mount Katahdin, Piscataquis County, and reported the collection of 20 species, which represent 14 genera and 11 families of spiders. Mount Katahdin is about 25 km southeast of our spruce-fir study area. Our collections of spiders from spruce-fir forests in Piscataquis County substantially adds to the species recorded from Maine.

Our results on mean catches of individuals and species per trap per week generally indicate that the ground-inhabiting spiders preferred the more open,

Fig. 4.—Mean species of spiders per trap per week; week 1 = 2 June 1977. Open triangles = dense spruce-fir stands; open circles = uncut residual strips; open squares = clearcut strips.



cleared habitats of clearcut strips to that of closed, shaded habitats of uncut residual strips and dense stands. Significantly more individuals and species were caught in the clearcut strips both study years (Table 2). However, most of this unequal distribution can be attributed to the greater abundance of lycosid spiders, and particularly *Pardosa* species, in the clearcut strips. For both study years, significantly more ($P \leq 0.05$) individuals of *Pardosa* species were trapped in the clearcut strips than in the other forest conditions, $\bar{X} = 8.4/\text{trap}/\text{week}$ in 1977 and $\bar{X} = 11.7/\text{trap}/\text{week}$ in 1978.

Measures of similarity among forest conditions indicated that more species (CC values) than individuals (PS values) shared forest conditions in common. No doubt heterogeneity of habitats and individual species requirements influenced the species composition and spatial distributions of spiders among the forest conditions studied. Species such as *Neoantistea magna*, *Pardosa mackenziana*, and *P. xerampelina* showed definite habitat affinities for clearcut strips; other species, such as *Wadotes calcaratus*, *Callobius bennetti*, *Lepthyphantes alpinus*, and *Xysticus canadensis* were intermediate in habitat association (i.e., two forest conditions, both similar); whereas, *Pocadicnemis americana* and *Trochosa terricola* were indeterminate regarding habitat preference.

Because species diversity and evenness of pitfall trap-catches were generally lower in clearcut strips both study years, we conclude that strip clearcutting may alter species richness and abundance of ground-dwelling spiders in northeastern spruce-fir forests. The open, cleared strips with abundant shrubs and forbs provide new and different habitats where hunting spiders (e.g., Lycosidae) abound. Coyle (1981) also found an abundance of hunting spiders in clearcuts of a southern Appalachian forest. The uncut residual stands of northern Maine, conversely, provide islands of "refugia" where spider populations are diverse. Thus, the overall effect of strip clearcutting (clearcut and uncut residual strips) is a reduction in species diversity and evenness of spiders (Table 3), but an increase in spider abundance (Table 2). With time and plant succession, the strip-clearcut areas should provide macrohabitats and microhabitats similar to dense stands.

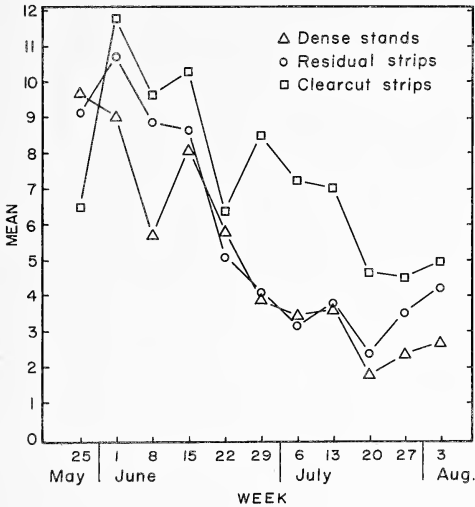


Fig. 5.—Mean species of spiders per trap per week; week 1 = 25 May 1978. Open triangles = dense spruce-fir stands; open circles = uncut residual strips; open squares = clearcut strips.

We detected little influence of either strip-clearcut age or litter depth on mean overall catches of individuals and species of spiders. However, strip-clearcut age may become increasingly important during later successional stages when forest regeneration causes canopy closure. Canopy closure, or absence thereof, apparently had a dramatic effect on the abundance and distribution of certain Lycosidae (e.g., species of *Pardosa*) in the northeastern spruce-fir forest. Most of the wolf spiders were found in open, sunny areas of clearcut strips, with lesser numbers in closed, shaded areas of dense stands and uncut residual strips. Bultman et al. (1982) also found a scarcity of wolf spiders in a beech-maple climax forest of western Michigan.

Several investigators (Hagstrum 1970; Uetz 1979; Bultman et al. 1982) have concluded that litter depth is an important factor that influences spider abundance, particularly in deciduous forests. We suspect that litter depth may have lesser influence on spider abundance in coniferous forests where litter structure tends to be fairly uniform. Absence of canopy closure probably has a more significant effect on overall spider abundance in spruce-fir forests, and particularly on the abundance of *Pardosa* species. Our results on species diversity (Table 3) and litter depth generally agree with Uetz (1979); i.e., species diversity increased with increased litter depth of uncut dense stands.

Based on pitfall-catch densities, spiders were abundant and active during the spruce budworm's early and late larval stages, and during budworm oviposition and dispersal of first instars (weeks 8-10). Spruce budworm oviposition generally spans 27 days in late June and July (Houseweart et al. 1982), and budworm eggs are susceptible to predation by arboreal spiders (Jennings and Houseweart 1978). After budworm eggs hatch (ca. 10 days), the young larvae disperse and seek overwintering sites. However, during dispersal many budworms are lost because the larvae land on nonhost vegetation (Morris and Mott 1963); they also are susceptible to predation by spiders (Mott 1963). Strip-clearcutting contributed to dispersal losses of early-instar budworms (Jennings et al. 1983). Results of the current study indicate that budworm larve landing in clearcut strips would be especially susceptible to attack by lycosid spiders because of the latter's great abundance. Predation on dropping late-instar budworms may also be significant

Table 3.—Spider species diversity and evenness of pitfall-trap catches by forest condition, Brillouin's formula, 1977 and 1978. 1977, 5 replicates each forest condition; 4 traps/replicate. 1978, 7 replicates (residual vs. clearcut strips); 3 replicates (residual + clearcut strips vs. dense stands); 4 traps/replicate.

| Forest condition | Diversity | | Evenness | |
|----------------------------|-----------|------|----------|------|
| | 1977 | 1978 | 1977 | 1978 |
| Residual strips | 1.31 | 1.37 | 0.81 | 0.81 |
| Clearcut strips | 0.98 | 1.08 | 0.57 | 0.58 |
| Residual + clearcut strips | 1.23 | 1.14 | 0.67 | 0.63 |
| Dense stands | 1.33 | 1.36 | 0.76 | 0.77 |

because mortality during the late larval stage influences generation survival of the spruce budworm (Morris 1963).

Additional studies are needed to determine the predatory roles of spiders in northeastern spruce-fir forests and their impacts on spruce budworm populations. Such studies will require assessment of both predator and prey densities, and specialized techniques, such as the ELISA assay (Fichter and Stephen 1979; Ragsdale et al. 1981), to determine numbers of spruce budworms eaten by spiders.

Enhancement of predator populations through forest management procedures is receiving increased attention (Crawford and Titterington 1979; Jennings and Crawford 1985). The current study indicates that populations of ground-dwelling spiders can be greatly increased by strip clearcutting; however, the long-term effects of strip clearcutting on changes in spider species diversity are unknown. Much more information is needed to develop sound, realistic pest management systems that promote and utilize natural agents of mortality and rely less on chemical insecticides.

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**TRIAENONYCHIDAE SUDAMERICANOS. III.
DESCRIPCION DE LOS NUEVOS GENEROS
NAHUELONYX Y VALDIVIONYX
(OPILIONES, LANIATORES)**

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ABSTRACT

Two new genera and a new species of Triaenonychidae are described from the valdivian wet forest of southern Argentina and Chile: *Nahuelonyx*, new genus, for *N. nasutus* (Ringuelet 1959), new combination and *Valdivionyx*, new genus, for *V. crassipes*, new species. The remarkable similarity in coloration of both species is mentioned.

RESUMEN

Dos nuevos géneros y una nueva especie de Triaenonychidae se describen del bosque húmedo valdiviano del sur de la Argentina y Chile: *Nahuelonyx*, género nuevo, para *N. nasutus* (Ringuelet 1959), combinación nueva y *Valdivionyx*, género nuevo, para *V. crassipes*, especie nueva. Se menciona la llamativa similitud de coloración en ambas especies.

INTRODUCCION

En un reciente trabajo sobre el género *Diasia* Sörensen 1902 (Maury, en prensa, a) mencioné que la especie que Ringuelet (1959) describió como *Diasia nasuta* debería ser ubicada en otro género. Un examen más minucioso de la serie típica de dicha especie (cinco ejemplares) me reveló la existencia de dos entidades distintas, muy diferentes a *Diasia*. Ambas pertenecen a la tribu Triaenonychini Sörensen 1902 y a mi juicio y de acuerdo a la literatura consultada, constituyen dos géneros nuevos para la ciencia, que he denominado *Nahuelonyx* y *Valdivionyx*. Abundante material de ambas formas proveniente del sur de la Argentina y Chile me ha permitido efectuar adecuadas diagnosis, en donde se consignan los caracteres que a mi parecer son de importancia sistemática; las variaciones intraespecíficas y esbozar un mapa de distribución geográfica. Ambos géneros son por el momento monotípicos y muy bien diferenciados por varios caracteres morfológicos y de genitalia, como puede verse en la clave adjunta. Lo que resulta sorprendente en dos géneros tan bien caracterizados es la singular semejanza en la coloración. En los opiliones Triaenonychidae no se le ha dado mucha importancia a este carácter, pero en este caso merece un somero comentario, por las implicaciones de orden biológico que puedan tener. Salvo

minimos detalles diferenciales, *Nahuelonyx* y *Valdivionyx* presentan un color castaño muy oscuro con veteado amarillento muy esfumado en cuerpo y apéndices; pero como carácter distintivo, muestran dos resaltantes manchas ocelares amarillo ocre en el prosoma, a los costados del tubérculo ocular. Por observaciones personales realizadas en el bosque húmedo valdiviano he comprobado que a diferencia de otros triaenoníquidos de la zona, de coloración críptica, *Nahuelonyx* y *Valdivionyx* (a veces se los encuentra en simpatria) son fácilmente detectables por estas manchas en los lugares donde habitan: reverso de troncos caídos o de cortezas y mantillo vegetal. Es de sospechar que dichas manchas cumplen alguna función. Pero como nada se conoce de la biología de estos opiliones, sólo se pueden hacer conjeturas sobre si la coloración similar y tan llamativa de estos dos géneros se debe a un parecido fortuito, a una evolución paralela o a algún caso de mimetismo.

La nomenclatura utilizada en la genitalia masculina es fundamentalmente la de un trabajo anterior (Maury y Roig Alsina 1985), pero a partir del presente artículo se emplea la traducción española de algunos términos: estilo (por stylus), laminilla (por lamella) y sensilo (por sensilia).

CLAVE PARA DIFERENCIAR *DIASIA*, *NAHUELONYX* Y *VALDIVIONYX*

1. Coloración general castaño amarillenta con manchas castaño oscuro; en el prosoma no hay manchas que se destaquen. Prosoma más largo que el escudo tergal. Borde anterior del prosoma sin hilera de tubérculos. Tubérculo ocular levemente cónico o romo, sin apófisis terminal. Metatarsos de las patas I a IV sin separación astrágalo/calcáneo.....*Diasia*
 Coloración general castaño muy oscura con jaspeado amarillento; dos manchas ocelares amarillo ocre en el prosoma. Prosoma igual o más corto que el escudo tergal. Borde anterior del prosoma con una hilera de tubérculos. Tubérculo ocular marcadamente cónico, con una apófisis terminal. Metatarsos de las patas I a IV con separación astrágalo/calcáneo 2
2. Metatarsos I a IV con el calcáneo mayor que el astrágalo. Tarsos III y IV similares en los dos sexos. Opérculo genital grande, de forma semicircular. Estigmas respiratorios parcialmente ocluidos. Tubérculo ocular con una larga apófisis terminal. Areas del escudo tergal con gruesas granulaciones. Pene indicado en las Figs. 11 a 13. Ovipositor con dos apófisis curvas laterales.....*Nahuelonyx*
 Metatarso I con el astrágalo igual que el calcáneo; metatarso II con el astrágalo menor que el calcáneo; metatarsos III y IV con el astrágalo mayor que el calcáneo. Tarsos III y IV del macho más engrosados que en la hembra. Opérculo genital pequeño, de forma ligeramente triangular. Estigmas respiratorios libres. Tubérculo ocular con corta apófisis terminal. Areas del escudo tergal con pequeñas granulaciones. Pene indicado en las Figs. 16 a 18. Ovipositor sin apófisis laterales.....*Valdivionyx*

Nahuelonyx, género nuevo

Diasia: Ringuelet 1959:256 (en parte, no *Diasia* Sörensen 1902).

Especie tipo.—*Nahuelonyx nasutus* (Ringuelet 1959), por monotipia.

Etimología.—El nombre genérico *Nahuelonyx* proviene de las palabras *Nahuel*, que en lengua indígena mapuche significa tigre y del griego *onyx*: uña.

Distribución.—Argentina: provincias de Neuquén y Río Negro; Chile: provincias de Cautín, Valdivia, Osorno, Llanquihue, Chiloé y Palena (Figs. 32-33).

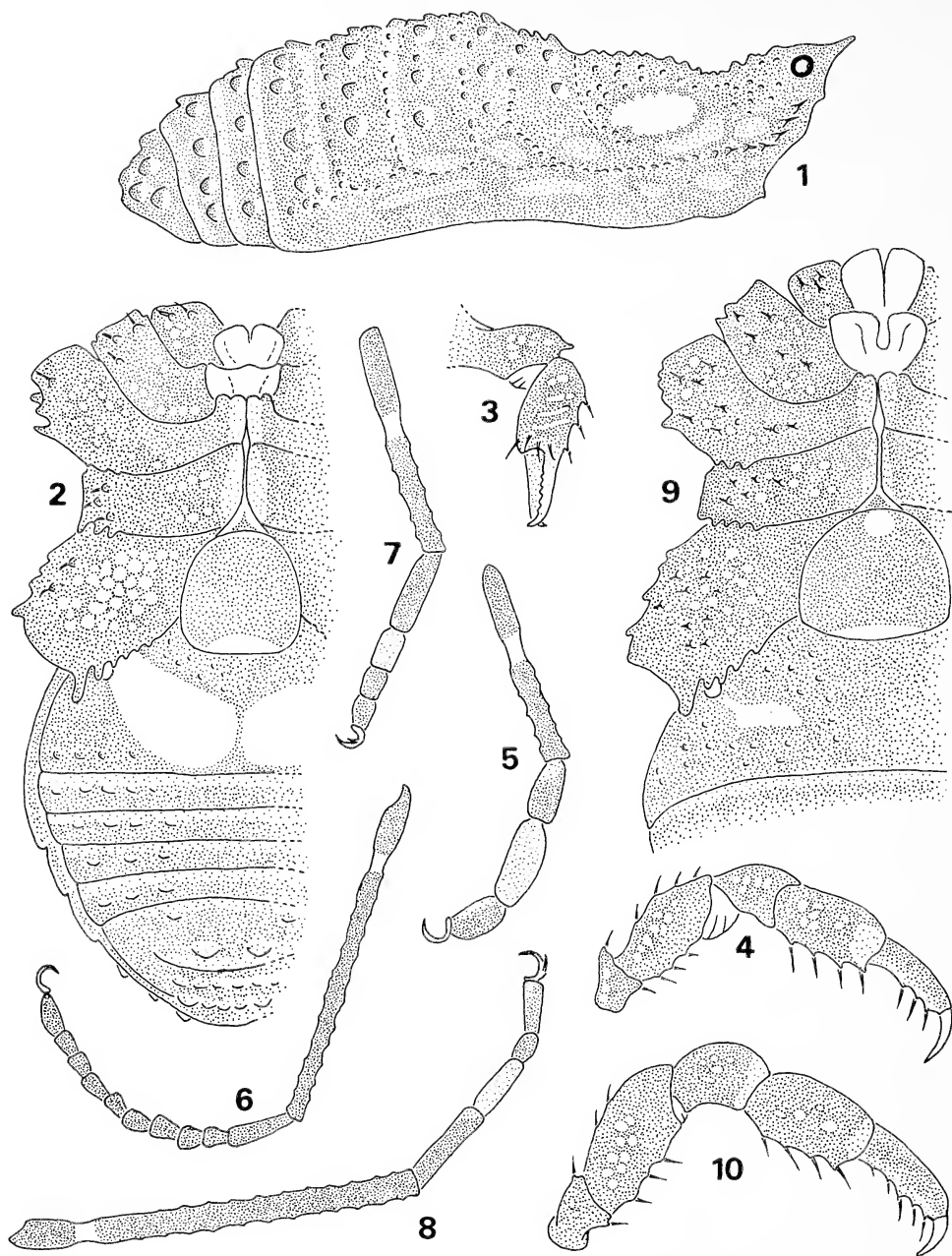
Diagnosis y descripción.—Triaenonychinae. Triaenonychini. Prosoma más corto que el escudo tergal. Tubérculo ocular elevado, cónico y con una aguda apófisis terminal. Prosoma con una hilera de tubérculos en todo el perímetro. Areas del escudo tergal poco definidas, inermes, con series transversales de gruesas granulaciones. Estigmas respiratorios parcialmente ocluidos por los tubérculos digitiformes del borde posterior de la coxa IV. Fémures de las patas I a IV granulados pero sin tubérculos que se destaquen. Opérculo genital de borde libre semicircular, ligeramente más ancho que largo en ambos sexos. Coxas I a IV con algunos pequeños tubérculos ventrales. Metatarsos I a IV con la separación astrágalo/calcáneo bien marcada por una zona anular deprimida e incolora; en todos los metatarsos, aunque en diferente proporción, el calcáneo es mayor que el astrágalo. En ambos sexos los tarsitos de la pata I ligeramente engrosados; en las otras patas normales. Distitarso de la pata I con dos segmentos; de la pata II con tres segmentos. Fórmula tarsal similar en los dos sexos: 3-7/11-4-4. Segmento basal de los quelíceros con una pequeña apófisis terminal dorsomedial. Dimorfismo sexual poco marcado: el opérculo genital es proporcionalmente más ancho que largo en la hembra que en el macho; en este último sexo hay dos áreas paramedianas postoperculares lisas y amarillentas, que no se ven en la hembra. Ovipositor bilobulado, con dos fuertes apófisis curvas laterales; hay cinco pares de sensilos ventrales y tres pares dorsoapicales. Pene con el estilo curvado hacia ventral; parte dorsolateral fuertemente bifurcada en su extremo distal, con un par de sensilos ventrales y una apófisis en la cara externa; la parte ventral lleva una laminilla hendida longitudinalmente, cuatro pares de sensilos y una apófisis lateral. Coloración general castaño muy oscuro con jaspeado amarillento; una gran mancha ocelar amarilla a cada lado del prosoma.

Nahuelonyx es, según la literatura consultada, el único triaenoníquido que posee en todos los metatarsos el astrágalo menor que el calcáneo. Este carácter, sumado a la coloración distintiva (sólo comparable a *Valdivionyx*) y a la peculiar morfología de la genitalia, permitirán individualizar a este nuevo género.

Nahuelonyx nasutus (Ringuelet 1959), combinación nueva
Figs. 1-15, 33

Diasia nasuta Ringuelet 1959:259-263 (en parte); figs. 32 a-b, 33 a-b.

Material típico.—Holotipo macho (MLP 24202) y paratipo hembra (MLP 24195): Lago Frías, Provincia de Río Negro, Argentina. El alotipo hembra y dos paratipos macho y hembra de la serie típica de *Diasia nasuta* pertenecen en realidad a *Valdivionyx crassipes*, género y especie nuevos.



Figs. 1-10.—*Nahuelonyx nasutus* (Ringuelet): 1-8, macho de Pirehueico; 1, cuerpo, vista lateral; 2, región coxoesternal (detalle); 3, quelícero derecho, vista lateral; 4, pedipalpo derecho, vista lateral; 5, metatarso y tarso I, vista lateral; 6, metatarso y tarso II, vista lateral; 7, metatarso y tarso III, vista lateral; 8, metatarso y tarso IV, vista lateral; 9-10, hembra de Pirehueico; 9, región coxoesternal (detalle); 10, pedipalpo derecho, vista lateral.

Diagnosis y descripción.—El material típico de esta especie se encuentra descolorido y en mal estado de conservación, especialmente el paratipo hembra. Los dibujos que se ofrecen en este trabajo corresponden a ejemplares de Pirehueico (MACN 8399 y 8400). Medidas en milímetros del holotipo macho en

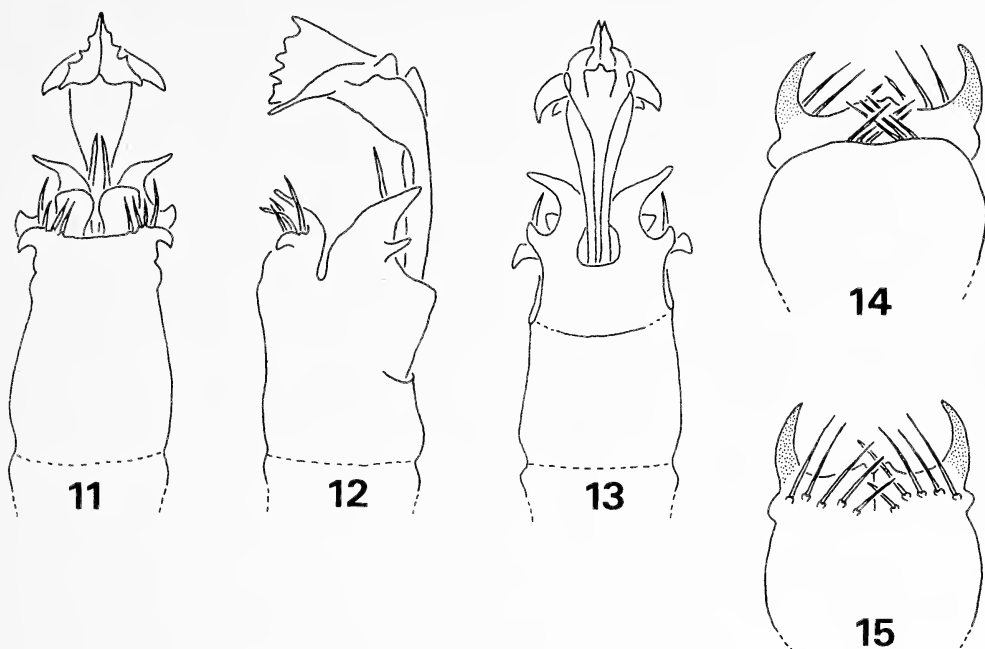
Tabla 1.—Tarsitos. Variabilidad en número en pata II.

| Número | Frecuencia | | | |
|--------|---------------------------|---------|------------------------------|---------|
| | <i>Nahuelonyx nasutus</i> | | <i>Valdivionyx crassipes</i> | |
| | Machos | Hembras | Machos | Hembras |
| 6 | 0 | 0 | 0 | 1 |
| 7 | 1 | 2 | 2 | 7 |
| 8 | 9 | 32 | 16 | 11 |
| 9 | 46 | 55 | 7 | 3 |
| 10 | 28 | 21 | 1 | 0 |
| 11 | 3 | 0 | 0 | 0 |

Tabla 2.—Medidas en milímetros.

| | <i>Nahuelonyx nasutus</i> | | <i>Valdivionyx crassipes</i> | |
|---------------------|---------------------------|--------|------------------------------|----------------|
| | Holotipo macho | Hembra | Holotipo macho | Alotipo hembra |
| Longitud total | 4.22 | 4.93 | 4.22 | 4.99 |
| Prosoma, longitud | 1.41 | 1.28 | 1.60 | 1.60 |
| ancho | 1.79 | 1.86 | 1.92 | 1.98 |
| Escudo, longitud | 1.79 | 2.24 | 1.79 | 1.98 |
| ancho | 2.37 | 3.01 | 3.01 | 3.20 |
| Pedipalpo, longitud | 2.87 | 3.07 | 3.78 | 3.97 |
| Trocánter | 0.32 | 0.32 | 0.45 | 0.45 |
| Fémur | 0.70 | 0.77 | 0.96 | 0.96 |
| Patela | 0.51 | 0.51 | 0.58 | 0.58 |
| Tibia | 0.64 | 0.70 | 0.83 | 0.83 |
| Tarso | 0.70 | 0.77 | 0.96 | 1.15 |
| Pata I, longitud | 5.76 | 5.70 | 6.59 | 6.59 |
| Trocánter | 0.45 | 0.51 | 0.51 | 0.58 |
| Fémur | 1.22 | 1.28 | 1.54 | 1.54 |
| Patela | 0.70 | 0.70 | 0.83 | 0.83 |
| Tibia | 1.02 | 1.66 | 1.22 | 1.15 |
| Metatarso | 1.22 | 1.15 | 1.28 | 1.28 |
| Tarso | 1.15 | 1.02 | 1.22 | 1.22 |
| Pata II, longitud | 8.58 | 8.20 | 9.78 | 9.54 |
| Trocánter | 0.51 | 0.58 | 0.70 | 0.70 |
| Fémur | 1.73 | 1.73 | 1.98 | 1.92 |
| Patela | 0.90 | 0.90 | 1.02 | 0.90 |
| Tibia | 1.41 | 1.34 | 1.60 | 1.54 |
| Metatarso | 1.98 | 1.92 | 2.11 | 2.05 |
| Tarso | 2.05 | 1.73 | 2.37 | 2.43 |
| Pata III, longitud | 6.08 | 5.96 | 6.85 | 6.78 |
| Trocánter | 0.58 | 0.58 | 0.70 | 0.70 |
| Fémur | 1.22 | 1.34 | 1.54 | 1.54 |
| Patela | 0.70 | 0.64 | 0.77 | 0.70 |
| Tibia | 1.15 | 0.90 | 1.09 | 1.22 |
| Metatarso | 1.41 | 1.41 | 1.34 | 1.34 |
| Tarso | 1.02 | 1.09 | 1.41 | 1.28 |
| Pata IV, longitud | 8.55 | 8.96 | 9.79 | 9.31 |
| Trocánter | 0.77 | 0.83 | 0.77 | 0.70 |
| Fémur | 1.66 | 1.73 | 2.11 | 1.92 |
| Patela | 0.96 | 0.96 | 0.96 | 0.96 |
| Tibia | 1.41 | 1.54 | 1.60 | 1.66 |
| Metatarso | 2.47 | 2.56 | 2.43 | 2.47 |
| Tarso | 1.28 | 1.34 | 1.92 | 1.60 |
| Quelícero, longitud | 1.86 | 1.98 | 2.37 | 1.92 |
| Segmento I | 0.77 | 0.77 | 0.96 | 0.83 |
| Segmento II | 1.09 | 1.21 | 1.41 | 1.09 |

la Tabla 2; la hembra medida proviene de Pirehueico (MACN 8400). La longitud total de los ejemplares estudiados varió entre 3.4 y 4.3 mm para los machos y 3.5 y 5.2 mm para las hembras; se observaron subadultos de hasta 3.4 mm de longitud. Coloración general castaño muy oscuro con jaspeado amarillento. En el prosoma se destacan, por detrás y a los costados del tubérculo ocular, dos manchas ocelares amarillo intenso (Fig. 1). El resto del prosoma y el escudo con manchado difuso; en algunos ejemplares hay manchas más definidas en los bordes laterales del escudo. Tergitos libres con manchado difuso; bordes libres amarillentos. Coxas, esternón y opérculo genital con fino tramado amarillento. En ambos sexos hay una mancha amarillo blancuzca en la zona de articulación del opérculo genital y, exclusivamente en el macho, dos manchas paramedianas postoperculares amarillentas, (Figs. 2, 9). Quelíceros y pedipalpos con fino puntillado amarillento. Trocánter, fémur, patela y tibia de las patas con fino puntillado amarillento; en los metatarsos el astrágalo es más oscuro que el calcáneo, especialmente en la pata IV; en todos los metatarsos la separación astrágalo/calcáneo marcada por una zona anular incolora (Figs. 5-8). En la pata I los tarsitos 1° y 3° oscuros y el 2° claro; en la II todos los tarsitos oscuros; en III y IV los tarsitos 1°, 3° y 4° oscuros, el 2° claro. Relación longitud prosoma: longitud escudo entre 1:1.23 y 1:1.76. Prosoma con algunas granulaciones dispersas por detrás del tubérculo ocular y un arco de tubérculos puntiagudos en todo el perímetro que se continúan, pero algo menos notables, en el escudo (Fig. 1). El tubérculo ocular, oblicuo en relación al eje del prosoma, es cónico y posee, además de unos pocos gránulos dispersos, una prominente apófisis apical. Areas del escudo marcadas por hileras transversales de gruesas granulaciones, entre las que se intercalan otras de menor tamaño. Tergitos libres con gruesas granulaciones. Esternitos y placa anal finamente granulados (Fig. 2). Coxa I con algunos gránulos ventrales pero sin tubérculos que se destaquen; coxas II a IV con unos pocos gránulos ventrales; la coxa IV con tubérculos digitiformes en el borde posterior. Segmento II del quelícero liso, con una serie de pelos rígidos en la cara dorsal (Fig. 3). Pedipalpos (Figs. 4, 10) muy chicos; trocánter con dos pequeñísimos tubérculos dorsales y uno ventral; fémur con dos o cuatro tuberculitos pilíferos dorsales y otros dos o tres ventrales; patela lisa; tibia con cuatro tuberculitos pilíferos en el borde ventral externo, cara ventral densamente pilosa; tarso con tres pares de pequeños tubérculos pilíferos, toda la cara ventral muy pilosa. Patas (Figs. 5-8): trocánter y fémur fuertemente granulados, pero sin tubérculos más destacados; patela y tibia algo menos granulados y metatarso finamente granuloso, excepto el anillo de separación astrágalo/calcáneo, que es liso. Las proporciones astrágalo/calcáneo en los metatarsos son las siguientes: pata I: 1:1.25; pata II: 1:4.50; pata III: 1:1.44 y pata IV: 1:4.71. Fórmula tarsal similar en los dos sexos: 3-7/11-4-4. En la Tabla 1 se ha indicado la variabilidad en el número de tarsitos de la pata II, separado por sexo. El ovipositor (Figs. 14-15) posee dos fuertes apófisis laterales, curvas y quitinizadas; hay cinco pares de sensilos ventrales y tres pares, algo más débiles, de sensilos dorsoapicales. Pene (Figs. 11-13): el glande muestra la parte dorsolateral bifurcada en su extremo distal en ramas fuertemente divergentes; en la cara lateral hay una apófisis triangular de vértice dirigido hacia el extremo distal y existe un par de gruesos sensilos ubicados en el centro, paralelos y ventrales al estilo. Una profunda escotadura anterior separa la parte dorsolateral de la parte ventral; esta última posee una apófisis lateral de vértice dirigido hacia el extremo basal; una laminilla



Figs. 11-15.—*Nahuelonyx nasutus* (Ringuelet): 11-13, macho de Pirehueico; 11, glande, vista ventral; 12, glande, vista lateral; 13, glande, vista dorsal; 14-15, hembra de Pirehueico; 14, ovipositor, vista dorsal; 15, ovipositor, vista ventral.

hendida longitudinalmente (la hendidura se ensancha hacia la base) y cuatro pares de sensilos: un par mayor ubicado en lateral de la laminilla y tres pares más chicos en ventral. El estilo se presenta suavemente curvado hacia la cara ventral, con el extremo de forma compleja, semejante a un cáliz.

Material estudiado.—ARGENTINA: Provincia de Neuquén; Lago Queñi, 2 XII 1985 (E. Maury), 1 macho (MACN 8397), Pucará, Lago Lacar, 20 km al O de San Martín de los Andes, 19 I 1972 (L. Herman), 2 juveniles (AMNH), 4 km al O de Pucará (900 m), 21 I 1972 (L. Herman), 1 juvenil (AMNH), camino entre Pucará y Laguna Venados, 24-25 I 1972 (L. Herman), 1 hembra y 2 juveniles (AMNH), Río Pucará, Lago Lacar, 13 I 1986 (L. Platnick, P. Goloboff y R. Schuh), 1 macho y 3 hembras (AMNH); Provincia de Río Negro; Puerto Blest, Lago Nahuel Huapi (770 m), 2 III 1979 (Misión Científica Danesa), 1 hembra (ZMC), Lago Frías, II 1950 (S. Coscarón y O. de Ferrariis), macho holotipo (MLP 24202) y hembra paratipo (MLP 24195) de *Diasia nasuta* Ringuelet. CHILE: Provincia de Cautín; Termas de Palquín, SE de Pucón, 17 I 1987 (E. Maury), 1 macho (MACN 8398); Flor del Lago, 15 km al NE de Villarica, 10 XI 1985 (S. y J. Peck), 1 macho (AMNH); Provincia de Valdivia; Pirehueico, 18 I 1985 (E. Maury), 1 macho (MACN 8399), 1 XII 1985 (E. Maury), 1 macho, 4 hembras y 1 juvenil (MACN 8400); Provincia de Osorno; Los Derrumbes, 5 km al S de Termas de Puyehue, 4-5 XII 1985 (E. Maury), 2 hembras (MACN 8401), Termas de Puyehue (180 m), 24 XI 1981 (N. Platnick y R. Schuh), 4 machos, 2 hembras y 5 juveniles (AMNH), 25 XI 1981 (N. Platnick y R. Schuh), 1 macho y 4 juveniles (AMNH), 1 km al E de Termas de Puyehue (305 m), 31 I 1985 (N. Platnick y O. Francke), 2 machos y 2 hembras (AMNH), Aguas Calientes, 28 I 1986 (N. Platnick y R. Schuh), 7 machos, 8 hembras y 1 juvenil (AMNH), Antillanca (720 m), 18-24 XII 1982 (A. Newton y M. Thayer), 1 juvenil (AMNH), 20-25 XII 1982 (A. Newton y M. Thayer), 1 hembra (AMNH); 4.1 km al E de Anticura (430 m), 19-26 XII 1982 (A. Newton y M. Thayer), 1 juvenil (AMNH), 19 XII 1984 al 6 II 1985 (S. y J. Peck), 4 hembras (AMNH), 1-11 I 1986 (L. Peña), 9 machos y 8 hembras (AMNH), 19-29 X 1985 (L. Peña), 12 machos y 21 hembras (AMNH), XII 1985 (L. Peña), 15 machos y 14 hembras (AMNH), Anticura-Repucura, 6 II 1985 (S. y J. Peck), 2 hembras (AMNH), colinas al S de Maicolpué (120 m), 30 I 1985 (N. Platnick y O. Francke), 1 hembra (AMNH); Provincia de Llanquihue; 5 km al S de Ensenada, 25 I 1986 (N. Platnick y R. Schuh), 1 macho (AMNH); Provincia de Chiloé; 5 km al N de Quellón (107 m), 1 XII 1981 (N.

Platnick y R. Schuh), 1 macho y 1 juvenil (AMNH), Chepu (7 m), 28 XII 1981 (N. Platnick y R. Schuh), 1 hembra (AMNH), 2 II 1985 (N. Platnick y R. Schuh), 1 macho (AMNH); Provincia de Palena; Chaitén (100 m), 4 XII 1981 (N. Platnick y R. Schuh), 1 macho y 1 juvenil (AMNH), vecindades de Chaitén, 5-7 XII 1981 (N. Platnick y R. Schuh), 1 macho (AMNH), 70 km al S de Chaitén, 16 I 1986 (N. Platnick, P. Goloboff y R. Schuh), 1 juvenil (AMNH); 22 km al NE de Puerto Ramírez, 2 XII 1986 (E. Maury), 1 juvenil (MACN 8402), 28.5 km al O de Futaleufú, 16 I 1986 (N. Platnick, P. Goloboff y R. Schuh), 1 macho y 1 juvenil (AMNH).

Valdivionyx, género nuevo

Diasia: Ringuelet 1959:256 (en parte, no *Diasia* Sörensen 1902).

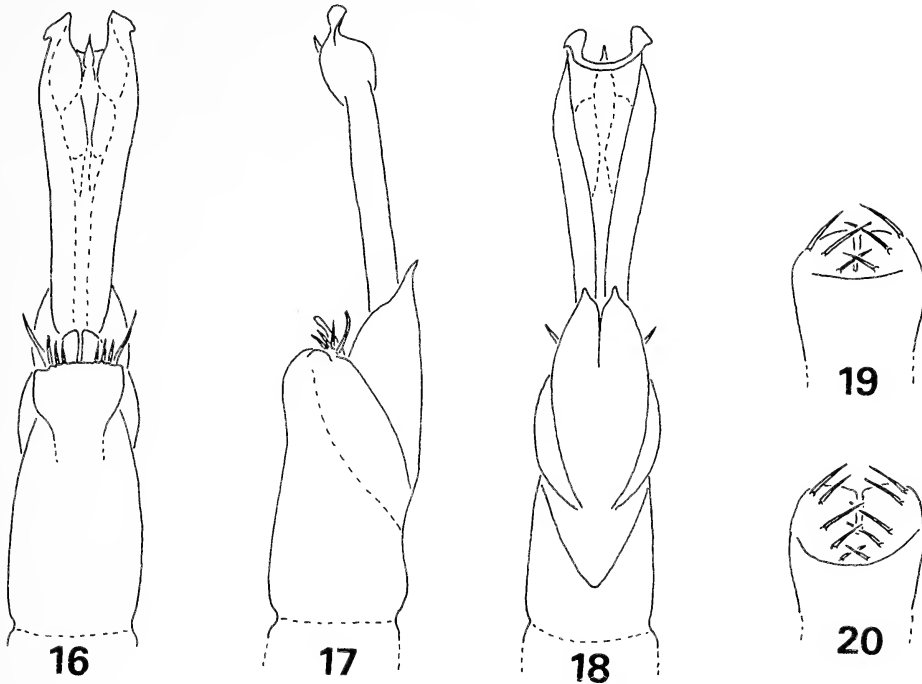
Especie tipo.—*Valdivionyx crassipes*, especie nueva, aquí designada.

Etimología.—El nombre genérico *Valdivionyx* proviene del nombre *Valdivia*, como referencia al habitat de este género, el bosque húmedo valdiviano y del griego *onyx*: uña.

Distribución.—Argentina: provincia de Río Negro; Chile: provincias de Osorno, Llanquihue, Chiloé y Palena (Figs. 32-33).

Diagnosis y descripción.—*Triaenonychinae*. *Triaenonychini*. Prosoma de igual largo o levemente más corto que el escudo tergal. Tubérculo ocular elevado, cónico, con una corta apófisis terminal. Prosoma con una serie de tubérculos aguzados en todo el perímetro. Areas del escudo tergal poco definidas, inermes, levemente insinuadas por algunas pequeñas granulaciones. Estigmas respiratorios libres, alejados del borde posterior de la coxa IV. Fémur de las patas I a IV ligeramente granuloso pero sin tubérculos que se destaquen. Opérculo genital de borde libre triangular. Coxas I a IV con algunos pequeños tubérculos ventrales. Metatarsos I a IV con la separación astrágalo/calcáneo bien marcada por una zona anular deprimida e incolora; pata I con el astrágalo de igual largo que el calcáneo, pata II con el astrágalo menor que el calcáneo, patas III y IV con el astrágalo mayor que el calcáneo. En ambos sexos, la pata I con los artejos del tarso ligeramente engrosados; en el macho las patas III y IV con los artejos del tarso muy engrosados. Distitarso de la pata I con dos segmentos; de la pata II con tres segmentos. Fórmula tarsal similar en los dos sexos: 3-6/10-4-4. Segmento basal de los quelíceros con una apófisis terminal dorsomedial. Dimorfismo sexual: macho con los tarsos de las patas III y IV más engrosados que en la hembra; con los pedipalpos más robustos, especialmente fémur y tibia y con el opérculo genital de forma más acusadamente triangular; hay además dos áreas paramedianas postoperculares lisas y amarillentas, ausentes en la hembra. Ovípositor bilobulado, con cinco pares de sensilos ventrales y tres pares dorsoapicales. Pene con el estilo derecho; parte dorsolateral levemente bifurcada en el ápice; parte ventral con una laminilla hendida longitudinalmente y con cuatro pares de sensilos. Coloración castaño muy oscura con jaspeado amarillento, una gran mancha ocelar amarilla a cada lado del prosoma.

Valdivionyx se asemeja mucho en la coloración al género *Nahuelonyx*, pero una buena cantidad de caracteres morfológicos y de genitalia los separan fácilmente, como puede verse en la clave adjunta. El único género conocido de triaenoníquido con una similar proporción de astrágalo/calcáneo en los metatarsos I a IV es *Triaenonychoides* H. Soares 1968. Este género, con dos especies (Maury, en prensa, b) es exclusivo de Chile y se distingue de *Valdivionyx* por su mayor tamaño y coloración parduzca; además macho y hembra presentan



Figs. 16-20.—*Valdivionyx crassipes*, especie nueva: holotipo macho; 16, glande, vista ventral; 17, glande, vista lateral; 18, glande, vista dorsal; 19-20, alotipo hembra; 19, ovipositor, vista dorsal; 20, ovipositor, vista ventral.

cuatro artejos tarsales en la pata I y, en el macho, los tarsos III y IV no muestran los segmentos engrosados como en *Valdivionyx*; la forma del tubérculo ocular y la armadura de los pedipalpos pueden ser otros caracteres distintivos.

***Valdivionyx crassipes*, especie nueva**

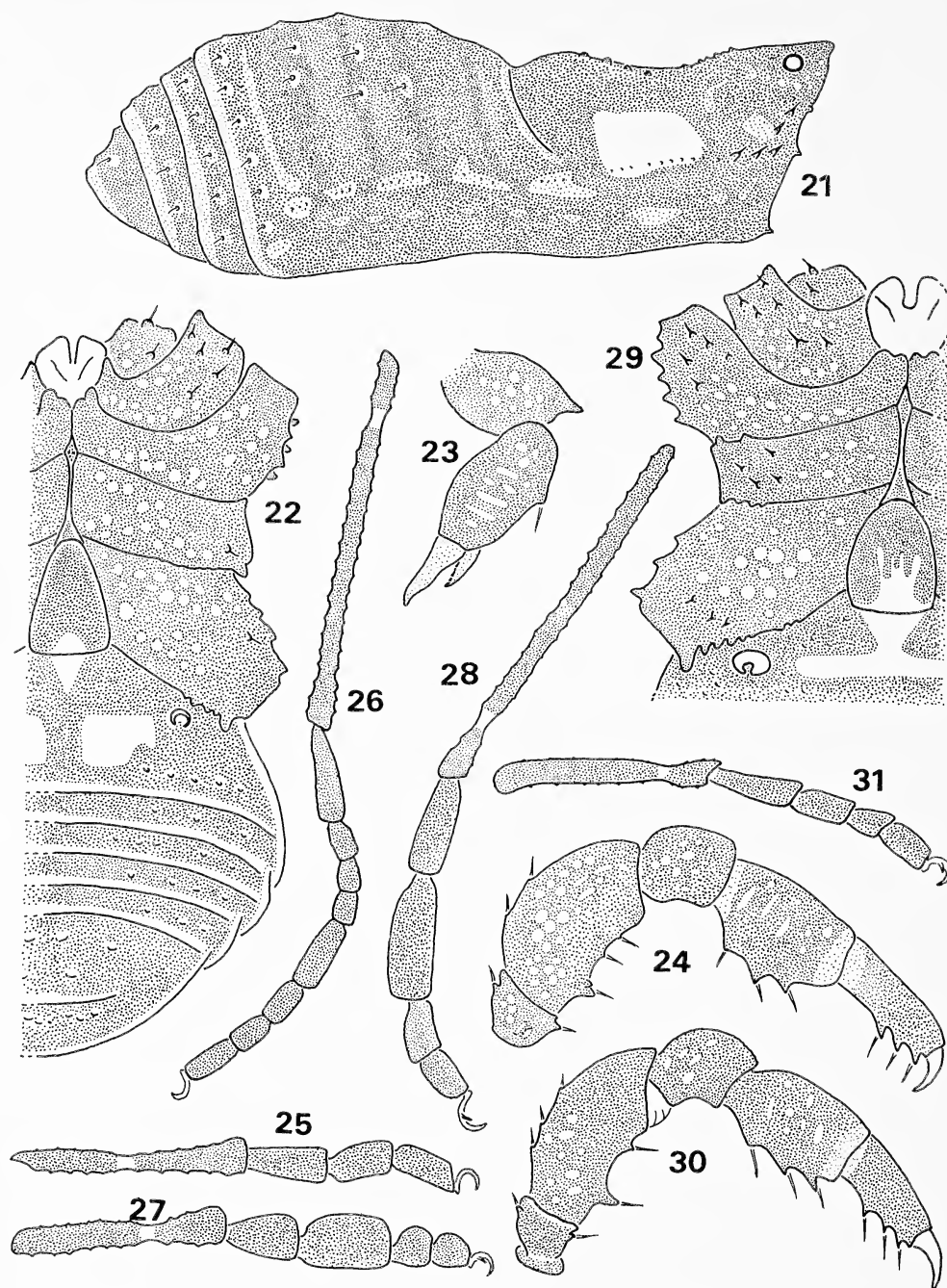
Figs. 16-33

Diasia nasuta: Ringuelet 1959:259 (en parte), figs. 32 c-d.

Material típico.—Holotipo macho (AMNH): Isla Tenglo, Puerto Montt, Provincia de Llanquihue, Chile; alotipo hembra (MACN 8403) y una hembra paratipo (MACN 8404): Termas de Pichicolo, Provincia de Palena, Chile; dos machos y dos hembras paratipos (AMNH) y dos machos paratipos (MACN 8405): Termas de Puyehue, Provincia de Osorno, Chile.

Etimología.—El nombre específico *crassipes* proviene del latín *crassus*: grueso y *pes*: pata, haciendo referencia al engrosamiento de los tarsos III y IV en el macho de esta especie.

Diagnosís y descripción.—Medidas en milímetros del material típico indicadas en la Tabla 2. La longitud total de los ejemplares estudiados varió entre 4.10 y 4.86 mm para los machos y 3.52 y 5.18 mm para las hembras; se observaron subadultos de hasta 3.14 mm de longitud. Colaración general castaño muy oscuro con jaspeado amarillento. En el prosoma se destacan, por detrás y a los costados del tubérculo ocular, dos manchas oclares amarillo intenso (Fig. 21). El resto del prosoma, así como el escudo, con manchas difusas; en algunos especímenes hay



Figs. 21-31.—*Valdivionyx crassipes*, especie nueva: 21-28, holotipo macho; 21, cuerpo, vista lateral; 22, región coxoesternal (detalle); 23, quelícero derecho, vista lateral; 24, pedipalpo derecho, vista lateral; 25, metatarso y tarso I, vista lateral; 26, metatarso y tarso II, vista lateral; 27, metatarso y tarso III, vista lateral; 28, metatarso y tarso IV, vista lateral; 29-31, alotipo hembra; 29, región coxoesternal (detalle); 30, pedipalpo derecho, vista lateral; 31, metatarso y tarso III, vista lateral.

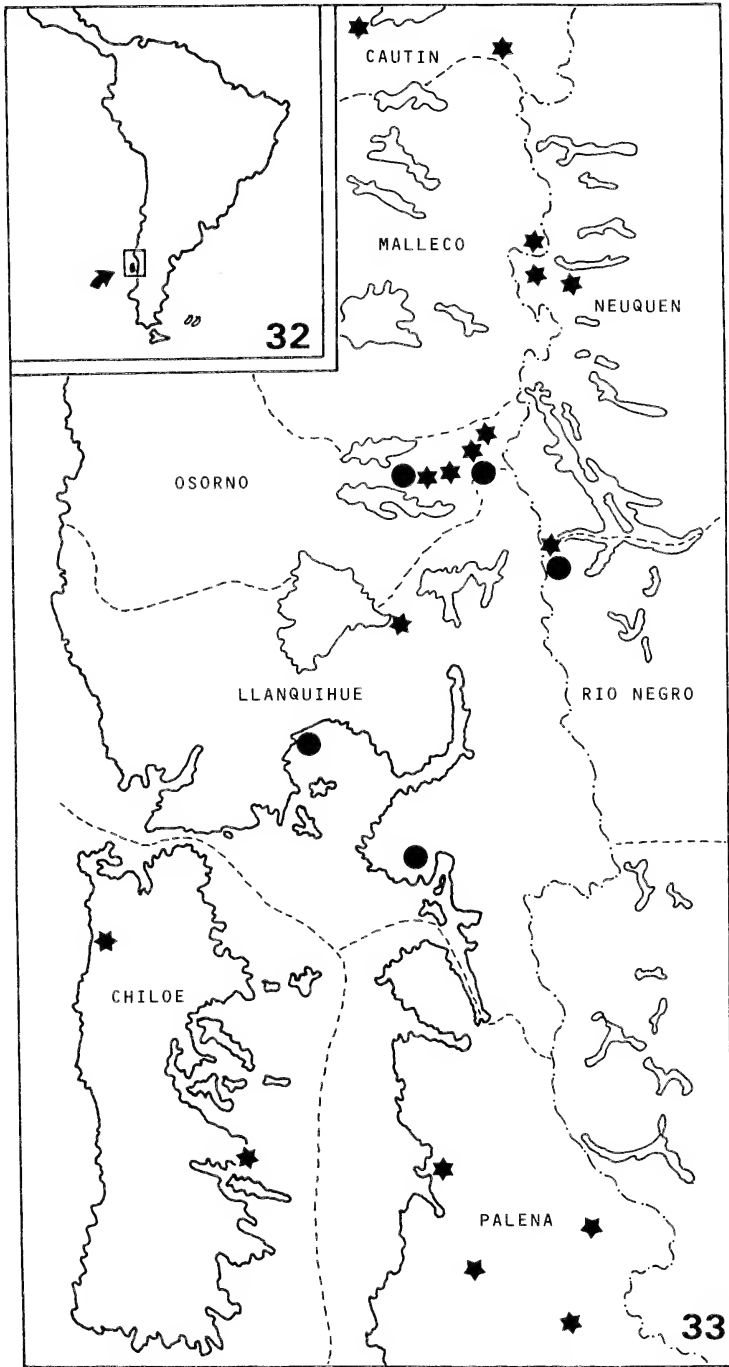


Fig. 32.—Ubicación del área estudiada. Fig. 33.—Localidades estudiadas de *Nahuelonyx nasutus* (Ringuelet) (estrellas) y de *Valdivionyx crassipes*, especie nueva (círculos).

manchas más definidas en los bordes laterales del escudo. Tergitos libres castaño oscuro con los bordes amarillentos. Coxas y esternón con fino tramado amarillento; opérculo genital con esfumado; esternitos con el borde amarillento. En ambos sexos hay una mancha amarillo blancuzca en la zona de articulación del opérculo genital y, exclusivamente en el macho, dos manchas paramedianas postoperculares amarillentas (Figs. 22-29). Quelíceros y pedipalpos con tramado amarillento. Trocánter, fémur, patela y tibia de las patas con tramado amarillento; metatarsos castaño esfumado; en todos los metatarsos la separación astrágalo/calcáneo marcada por un anillo de color más claro; en el astrágalo IV se nota una pseudoarticulación de color levemente más pálido (Fig. 28). Tarsitos de todas las patas con esfumado castaño. Relación longitud prosoma : longitud escudo entre 1:1 y 1:1.25. En el prosoma, detrás del tubérculo ocular, hay dos hileras longitudinales de granulaciones, levemente curvadas hacia medial; además de un arco de tubérculos puntiagudos, espaciados, en todo el perímetro. El tubérculo ocular, oblicuo en relación al eje del prosoma, es cónico y remata en una corta apófisis roma apical; hay también algunos granulitos dispersos. Areas del escudo casi lisas, con algunas pequeñas granulaciones pilíferas (Fig. 21). Tergitos libres, esternitos y placa anal con granulitos esparcidos (Figs. 22-29). Coxa I con algunos gránulos ventrales, los mayores se disponen cerca del borde anterior; coxas II a IV con algunos gránulos dispersos; la coxa IV con tubérculos digitiformes en el borde posterior. Segmento II del quelíceros casi liso, con algunos granulitos pilíferos en la cara dorsal (Fig. 23). Pedipalpos (Figs. 24, 30) relativamente pequeños, algo más robustos en el macho, especialmente fémur y tibia. Trocánter con dos granulitos dorsales y uno ventral; fémur casi liso dorsalmente, con dos o tres pequeñísimos granulitos pilíferos; borde ventral con tres tubérculos más prominentes, sobre todo el basal que es aguzado; patela lisa; tibia con tres fuertes tubérculos pilíferos en el borde ventral externo y uno en el borde ventral interno; tarso con tres tuberculitos pilíferos en el borde ventral externo y dos en el borde ventral interno. Patas (Figs. 22-28, 31): trocánter, fémur, patela y tibia con algunas granulaciones pero sin tubérculos que se destaquen; metatarso finamente granuloso, excepto el anillo de separación astrágalo/calcáneo, que es liso. Las proporciones astrágalo:calcáneo en los metatarsos son las siguientes: pata I: 1:1; pata II: 1:5.20; pata III: 1:0.50 y pata IV: 1:0.26. Fórmula tarsal similar en los dos sexos: 3-6/10-4-4. En la Tabla 1 se ha indicado la variabilidad en el número de tarsitos de la pata II, separado por sexo. Ovipositor (Figs. 19-20) bilobulado, con cinco pares de sensilos ventrales y tres pares dorsoapicales. Pene (Figs. 16-18): el glande presenta la parte dorsolateral levemente bifurcada en el ápice, terminando en dos pequeñas apófisis; parte ventral con la laminilla hendida longitudinalmente y con cuatro pares de sensilos: un par mayor ubicado lateralmente a la laminilla y tres pares algo más chicos ubicados ventralmente; el estilo es recto, ensanchándose levemente en el tercio distal.

Material estudiado.—ARGENTINA: Provincia de Río Negro; Lago Frías, febrero de 1950 (S. Coscarón y O. de Ferrariis), hembra alotipo (MLP 24378), 1 macho y 1 hembra paratipos (MLP s/n) de *Diasia nasuta* Ringuelet. CHILE: Provincia de Osorno; Termas de Puyehue (180 m), 24 XI 1981 (N. Platnick y R. Schuh), 2 machos y 2 hembras paratipos (AMNH), 2 machos paratipos (MACN 8405), 12 III 1965 (H. Levi), 2 machos y 1 hembra (MCZ), 10 km al E de Puyehue, 24 I 1951 (E. Ross y A. Michelbacher), 4 machos (CAS), Parque Nacional Puyehue, ruta a Antillanca (470 m), 20-25 XII 1982 (A. Newton y M. Thayer), 1 hembra (AMNH), 18-24 XII 1982 (A. Newton y M. Thayer), 1 macho y 1 hembra (AMNH), Los Derrumbes, 5 km al S de Termas de Puyehue, 4-5 XII 1985 (E.

Maury), 2 hembras y 1 juvenil (MACN 8406), Anticura, XII 1985 (L. Peña), 1 macho (AMNH): Provincia de Llanquihue; Isla Tenglo, Puerto Montt, 9 III 1962 (A. Archer), macho holotipo (AMNH): Provincia de Chiloé; Isla Chiloé, 15-18 XII 1985 (L. Peña), 1 macho (AMNH): Provincia de Palena; Termas de Pichicolo, 11 km al O de Río Negro, 8-9 XII 1985 (E. Maury), hembra alotipo (MACN 8403), 1 hembra paratipo y 1 juvenil (MACN 8404).

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SPIDERS (ARANEAE) CAPTURED IN MALAISE TRAPS IN SPRUCE-FIR FORESTS OF WEST-CENTRAL MAINE

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ABSTRACT

Spiders of 12 families, 20 genera, and 25 species were captured in modified Malaise traps deployed in spruce-fir forests of Somerset and Piscataquis Counties, Maine. Numbers of species and individuals differed between web-spinner and hunter foraging strategies. Sørensen's similarity quotient (QS) indicated that the Malaise-trapped fauna had greater similarity to arboreal than to terrestrial spider faunas of northeastern spruce-fir forests. Spider-trap interactions include accidental capture and possibly attraction; attractive features include trap architecture, concentrated potential prey, and protective shelter.

INTRODUCTION

Malaise traps (Malaise 1937) and modified versions (Gressitt and Gressitt 1962; Butler 1965; Townes 1962, 1972) primarily were designed for capture of flying insects. Such traps have been acclaimed, "one of the major advances in collecting methods in this century" (Steyskal 1981, p. 225). Malaise-trap captures include numerous species of Diptera, Hymenoptera, and Lepidoptera, with lesser numbers of Heteroptera and Coleoptera (Townes 1972). Other insect orders and arthropod classes including spiders (Arachnida, Araneae) also are trapped; however, to our knowledge Malaise traps have not been purposefully used to collect spiders.

During investigations of insecticidal impacts on terrestrial nontarget organisms (Hilburn 1981), modified Malaise traps were deployed in spruce-fir forests of west-central Maine. The forests were infested with the spruce budworm,

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Fig. 1.—Modified Malaise trap for capturing insects and spiders in spruce-fir forests, west-central Maine.

Choristoneura fumiferana (Clemens), the most destructive defoliator of conifers in the northeastern United States and Canada (Kucera and Orr 1981). Numerous insects and fewer spiders were captured in the Malaise traps; insect captures were summarized by Hilburn (1981). In this paper we describe the Malaise-trapped spiders, compare the trapped fauna with terrestrial- and arboreal-spider faunas of northeastern forests, and identify possible spider-Malaise trap interactions.

METHODS

Spiders were collected in 12 Malaise traps deployed at 12 sampling sites (1 trap/site) in spruce-fir forests of west-central Maine near Moosehead Lake. Three sites were in Somerset County; nine were in Piscataquis County. For details of sampling sites and sampling protocol, see Hilburn (1981) and Hilburn and Jennings (1988).

The Malaise traps were modifications of Townes' (1972) design and were placed on the ground in the herb-shrub layer (Fig. 1). Spiders and insects were captured in 1-pint (0.47-liter) jars containing 70% ethyl alcohol as a killing-preservative agent. Captured specimens were sorted and identified in the laboratory. Although there were six 48-h sampling periods for each site, collected spiders were combined from all sites and over all sampling dates (21 May to 29 June 1980).

Spiders were identified by the senior author; species determinations follow Kaston (1981) and other consulted sources including: Opell and Beatty (1976) for the Hahniidae; Leech (1972) for the Amaurobiidae; Chamberlin and Gertsch (1958) for the Dictynidae; Dondale and Redner (1982) for the Clubionidae; and Dondale and Redner (1978) for the Philodromidae and Thomisidae. Sexually

mature spiders were identified to species; most juveniles, including penultimate males, were identified to generic level. However, juveniles of *Philodromus* spp. were assigned to species group based on carapace and leg markings (Dondale and Redner 1978); a single juvenile of *P. placidus* Banks was identified to species based on characteristic leg markings.

Chi-square analysis (χ^2 , $P = 0.05$) was used to test the null hypothesis of equal spider distribution (individuals) between foraging strategies (web spinner, hunter). Because web spinners generally are more sedentary and less mobile than hunters, we suspected that Malaise-trap catches may be biased toward capture of hunters. Sørensen's similarity quotient (QS), as defined by Price (1975, p. 341), was used to compare habitat associations (terrestrial, arboreal) for the Malaise-trapped spiders. The formula used was: $QS = 2C \times 100 / (A + B)$, where A is the number of species observed in this study, B is the number of species in the compared study (e.g., Loughton et al. 1963), and C is the number of species common to both studies. Because sampling methods and intensities varied considerably among studies, the calculated QS values give only general indications of faunal affinities, not absolute associations. The comparisons were limited to spider-faunal studies of northeastern forests having spruce (*Picea* spp.) and fir (*Abies balsamea* (L.) Mill.) components.

RESULTS AND DISCUSSION

Spider taxa.—Spiders of 12 families, 20 genera, and at least 25 species were collected in Malaise traps deployed in spruce-fir forests of west-central Maine (Table 1). Species composition differed by foraging strategy; species of web spinners were more prevalent (56.0% of total species) than species of hunters (44.0%). Species richness per family ranged from one (Hahniidae, Dictynidae, Thomisidae) to four (Salticidae).

Spider numbers.—Of 86 total specimens collected, most (46.5%) were males; juveniles (32.6%) and females (20.9%) comprised the remainder. Four penultimate males were included in the juvenile category. The abundance of males is probably the result of greater male sexual-cursorial activity (Muma and Muma 1949); male spiders may move considerable distances in search of females. Individuals were distributed unevenly by foraging strategy, i.e., more hunters (54.6% of total specimens) were caught in the Malaise traps than web spinners (45.4%). However, the uneven distribution of individuals was not statistically significant ($\chi^2 = 0.74$, $df = 1$, $P > 0.05$) between foraging strategies.

Males and females of the sac spider *Clubiona canadensis* Emerton were by far the most commonly collected spider in the Malaise traps; this species accounted for 25.6% of all specimens.

Habitat associations.—Most of the species of spiders taken in Malaise traps have been collected in other northeastern spruce-fir forests (Loughton et al. 1963; Renault 1968). Comparisons with previous spider-faunal studies indicated that the Malaise-trapped fauna had greater similarity (i.e., higher QS values) to the arboreal fauna than to the terrestrial fauna of northeastern forests (Table 2). And, by definition ($QS < 50$; Price 1975) the Malaise-trapped fauna was distinct from all compared terrestrial and arboreal faunas. The relatively low similarity ($QS = 11.5$) between pitfall collections (Hilburn and Jennings 1988) and Malaise-trap

Table 1.—Species and numbers of spiders (Araneae) in Malaise traps, spruce-fir forests of west-central Maine, 1980.

| FAMILY | SPECIES AND NUMBER |
|----------------|--|
| WEB SPINNERS | |
| HAHNIIIDAE | <i>Antistea brunnea</i> (Emerton) 1 female |
| AMAUROBIIIDAE | <i>Amaurobius borealis</i> Emerton 1 male |
| | <i>Callobius bennetti</i> (Blackwall) 3 males |
| DICTYNIDAE | <i>Dictyna phylax</i> Gertsch & Ivie 1 male |
| THERIDIIDAE | <i>Theridion differens</i> Emerton 2 males |
| | <i>Theridion pictum</i> (Walckenaer) 1 female |
| | <i>Theridion</i> spp. 1 penult. male, 3 juv. |
| LINYPHIIDAE | <i>Frontinella pyramitela</i> (Walckenaer) 1 juv. |
| | <i>Microlinyphia mandibulata</i> (Emerton) 1 female |
| ERIGONIDAE | <i>Dismodicus bifrons decemoculatus</i> (Emerton) 2 males, 4 females |
| | <i>Hypselistes florens</i> (O.P.-Cambridge) 1 male, 2 females |
| | Undet. spp. 1 penult. male, 3 juv. |
| ARANEIDAE | <i>Araneus</i> sp. 1 juv. |
| | <i>Araniella displicata</i> (Hentz) 1 male |
| | <i>Nuctenea</i> sp. 1 juv. |
| TETRAGNATHIDAE | <i>Tetragnatha versicolor</i> Walckenaer 2 females |
| | <i>Tetragnatha</i> sp. 1 penult. male, 5 juv. |
| HUNTERS | |
| CLUBIONIDAE | <i>Clubiona canadensis</i> Emerton 17 males, 5 females |
| | <i>Clubiona kastoni</i> Gertsch 1 male |
| | <i>Clubiona trivialis</i> C. L. Koch 1 male, 1 female |
| | <i>Clubiona</i> spp. 1 penult. male, 6 juv. |
| PHILODROMIDAE | <i>Philodromus exilis</i> Banks 3 males |
| | <i>Philodromus placidus</i> Banks 1 juv. |
| | <i>Philodromus</i> spp. (<i>rufus</i> group) 2 juv. |
| | <i>Tibellus oblongus</i> (Walckenaer) 3 males |
| THOMISIDAE | <i>Misumena vatia</i> (Clerck) 2 males |
| SALTICIDAE | <i>Eris</i> sp. 1 juv. |
| | <i>Metaphidippus flavipedes</i> (G. & E. Peckham) 1 male |
| | <i>Metaphidippus protervus</i> (Walckenaer) 1 female |
| | <i>Sitticus finschii</i> (L. Koch) 1 male |

collections at the *same* study sites support this conclusion. The Malaise-trap spiders probably are representative of the intermediate herb-shrub layer; however, comparative studies are lacking for these strata.

Some of the Malaise-trapped species are commonly associated with terrestrial habitats; others are commonly associated with arboreal habitats. The amaurobiids, *Amaurobius borealis* Emerton and *Callobius bennetti* (Blackwall), frequently are found on or near the ground (Kaston 1981); *C. bennetti* also occurs under loose bark of spruce and fir trees killed by the spruce budworm (Jennings, unpubl. data), and on foliage of balsam fir (Loughton et al. 1963). Likewise, *Dictyna phylax* Gertsch & Ivie, *Araniella displicata* (Hentz), *Philodromus exilis* Banks, *P. placidus*, and *Metaphidippus flavipedes* (G. & E. Peckham) are most commonly found on foliage of conifers (Renault 1968; Dondale and Redner 1978; Jennings and Collins 1987b); rarely are these species found on the ground. A related species of *Philodromus*, *P. lutulentus* Gertsch, has been taken in Malaise traps elsewhere (Dondale and Redner 1978).

Table 2.—Comparison of Malaise-trapped spiders with terrestrial and arboreal spider faunas of northeastern forests (QS = Sørensen's Similarity Quotient).
*Species list incomplete.

| Habitat | Sampling Method | Forest Community | Locality | QS | Source |
|-------------|----------------------|-------------------------|--|------|----------------------------|
| Terrestrial | Pitfall traps | Mixed boreal | Shebandowan, Ontario | 6.0 | Freitag et al. 1969 |
| Terrestrial | Pitfall traps | Red spruce stand | University Forest, New Brunswick | 14.6 | Carter & Brown 1973* |
| Terrestrial | Pitfall traps | Fir-spruce | Elmsville and Priceville, New Brunswick | 14.3 | Varty & Carter 1974* |
| Terrestrial | Pitfall traps | Spruce-fir | Piscataquis County, Maine | 9.4 | Jennings et al. 1988 |
| Terrestrial | Pitfall traps | Spruce-fir | Somerset and Piscataquis Counties, Maine | 11.5 | Hilburn & Jennings 1988 |
| Arboreal | Pole-pruned branches | Fir-spruce (Balsam fir) | Green River Watershed, New Brunswick | 27.8 | Loughton et al. 1963 |
| Arboreal | Pole-pruned branches | Fir-spruce (Balsam fir) | Green River Watershed, New Brunswick | 23.6 | Renault (1968) |
| Arboreal | Pole-pruned branches | Spruce-fir (Red spruce) | Piscataquis County, Maine | 30.4 | Jennings & Collins (1987a) |

A few of the Malaise-trapped spiders in west-central Maine are known to frequent both terrestrial and arboreal habitats or intermediate herb-shrub strata. The sac spider *Clubiona canadensis* Emerton has been taken in pitfall traps, under stones, and in leaf litter (Dondale and Redner 1982); this species also occurs on foliage of red spruce, *Picea rubens* Sarg. (Jennings and Collins 1987a), and balsam fir (Loughton et al. 1963; Renault 1968). Specimens of *C. trivialis* are common inhabitants of spruce, fir, and pine (*Pinus*) foliage, but also are found under loose bark, under stones, and in leaf litter. Another species of sac spider, *Trachelas tranquillus* (Hentz), has been taken "in the folds and crevices of Malaise traps" (Dondale and Redner 1982, p. 126); Platnick and Shadab (1974) also report this species from Malaise traps. The crab spider *Misumena vatia* (Clerck) has been collected commonly on flowers and foliage of many herbs, shrubs, and deciduous trees (Dondale and Redner 1978), and coniferous trees (Jennings and Collins 1987b). *Tibellus oblongus* is usually found in tall grass (Dondale and Redner 1978), and occasionally in pitfall traps (Varty and Carter 1974; Jennings et al. 1988).

Species of Hahniidae are small spiders that spin delicate sheet webs near the ground (Kaston 1981). *Antistea brunnea* (Emerton) has been taken by pitfall traps in spruce-fir forests of Maine (Jennings et al. 1988; Hilburn and Jennings 1988), but not from the tree canopy layer. The erigonids also are small spiders that live chiefly under dead leaves near the ground (Kaston 1981); however, some species, e.g., *Hypselistes florens* (O. P.-Cambridge), are taken in large numbers by sweeping bushes and grasses (Kaston 1981), and on foliage of balsam fir (Loughton et al. 1963; Renault 1968).

Both species of comb-footed spiders captured in the Malaise traps, *Theridion differens* Emerton and *T. pictum* (Walckenaer), are common inhabitants of conifers (Renault 1968; Kaston 1981); however, *T. differens* also occurs in grass and low bushes (Kaston 1981). The bowl and doily spider, *Frontinella pyramitela* (Walckenaer), spins a characteristic sheet web in low branches, bushes, and tall grass (Kaston 1981), and on foliage of balsam fir (Loughton et al. 1963; Renault 1968). The platform spider, *Microlinyphia mandibulata* (Emerton), spins a platform-like sheet web, "usually in grass two to six inches from the ground," (Kaston 1981, p. 124); however, this species also has been taken on foliage of balsam fir (Renault 1968).

Notably absent from the Malaise-trap collections in west-central Maine were species of Agelenidae, Gnaphosidae, and Anyphaenidae. The agelenid funnel-weavers are frequently taken in pitfall traps (Carter and Brown 1973; Jennings et al. 1988; Hilburn and Jennings 1988) and on coniferous-tree foliage (Loughton et al. 1963; Renault 1968) in northeastern forests. Species of *Coelotes* and *Wadotes* are found under loose bark and stones; species of *Agelenopsis* spin their funnel webs in grasses and on bushes (Kaston 1981). Gnaphosid spiders also are frequently taken in pitfall traps in northeastern spruce-fir forests; species of *Haplodrassus* and *Zelotes* have been taken on foliage of balsam fir (Loughton et al. 1963; Renault 1968). Gnaphosid species reported taken in Malaise traps include: *Drassodes saccatus* (Emerton) (Platnick and Shadab 1976); *Herpyllus ecclesiasticus* Hentz (Platnick and Shadab 1977); *Nodocion floridanus* (Banks) (Platnick and Shadab 1980a); and *Cesonia bilineata* (Hentz) (Platnick and Shadab 1980b). *Sergiolus cyaneiventris* Simon has been collected "in insect flight traps," (Platnick and Shadab 1981). Of these gnaphosid species, only *H. ecclesiasticus* has been recorded from Maine.

Spiders of the family Anyphaenidae are long-legged active hunters (Dondale and Redner 1982); some inhabit foliage of trees and shrubs, others are found in leaf litter and in crevices under logs and stones on the forest floor. Interestingly, none have been taken in pitfall traps or in foliage samples from northeastern spruce-fir forests. Species of anyphaenids recorded taken in Malaise traps include: *Aysha gracilis* (Hentz), *Wulfila saltabundus* (Hentz), *Anyphaena pectorosa* L. Koch, and *Anyphaena aperta* (Banks), all reported by Dondale and Redner (1982); *Anyphaena maculata* (Banks), *Anyphaena pectorosa*, *Anyphaena fraterna* (Banks), and *Wulfila alba* (Hentz), all reported by Platnick (1974). Only *W. saltabundus* has been taken in Maine and Nova Scotia; the other species have more southern distributions (Platnick 1974; Dondale and Redner 1982).

Spider-trap interactions.—Are spiders attracted to Malaise traps? Or, is their presence in these traps accidental? Based on numbers and species collected during this study, we suggest that the interactions of spiders with Malaise traps may be more than accidental. Although some initial encounters with Malaise traps may be accidental, we suspect that spiders respond favorably to attractive features of a suitable habitat. However, this hypothesis needs testing under controlled conditions.

Three possible features that may influence attraction of spiders to Malaise traps are: (1) the physical architecture of the traps, (2) the presence of abundant potential prey, and (3) the sheltered protection from the elements and from natural enemies. Spiders respond to structural features within habitats (Greenquist and Rovner 1976) and many species colonize man-made structures (Fowler 1980; Robinson 1981; Streit and Roser-Hosch 1982; Stevenson and Dindal 1981) and man-made environments (Duffey 1975). There is increasing evidence that structural features within habitats play important roles in habitat selection by spiders (Riechert and Gillespie 1986). Spiders also respond to increases in prey density (Riechert and Gillespie 1986), and abundance of prey influences habitat selection (Turnbull 1964; Riechert and Luczak 1982). Because Malaise traps attract numerous flying insects, especially Diptera, Hymenoptera, and Lepidoptera (Townes 1962), these traps are sources of aggregated prey density. Spiders respond to aggregations of prey (MacKay 1982; Riechert 1976). We suspect that spiders may be attracted to concentrations of insects, especially near the apex and catchment jar of Malaise traps. For Malaise-trap maintenance, Martin (1977, p. 27) advises, "look inside the trap, especially the entrance to the killing bottle, for spider webs, which must be removed and the spiders captured and killed, if possible." In Maine, Hilburn observed spider webbing near the apex of a Malaise trap without catchment jar; the web was positioned to capture insects exiting from the trap.

Avoidance of predators also affects habitat selection by spiders (Riechert and Gillespie 1986). In this respect, Malaise traps may provide spiders temporary shelter and protection from their natural enemies, such as birds and predatory wasps (Pompilidae and Sphecidae). The traps also may provide shelter from rain and extremes of temperature.

CONCLUSION

Although Malaise traps are widely used for capture of flying insects (see Steyskal (1981) for a bibliography on Malaise traps), rarely are spiders recorded

among the captured fauna. We found only two previous studies (Wilkinson et al. 1980; Hauge and Midtgaard 1986) that included spiders among Malaise-trap captures. A few isolated records of individual species taken in Malaise traps are found in the araneological literature (e.g., Dondale and Redner 1982; Platnick 1974; Platnick and Shadab 1976, and others); most records concern species of Anyphaenidae, Clubionidae, and Gnaphosidae. We suspect that spiders may occur more commonly in Malaise-trap collections than is reported in the entomological-araneological literature. The sparsity of published information on Malaise-trapped spiders may be due to the failure of investigators to collect, identify, and report such captures. Personal communications with investigators who frequently use Malaise traps support these conclusions; both Robert W. Matthews and Richard H. Roberts have observed spiders in their Malaise traps on numerous occasions, but the spiders were not collected and identified.

Finally, Malaise traps may supplement (but not supplant) other methods used for collecting and sampling spiders, especially for species in the herb-shrub layer. Malaise traps also may be useful for testing hypotheses concerning aggregation responses of spiders to increased prey densities.

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REPRODUCTIVE PERIODS OF *PHIDIPPUS* SPECIES (ARANEAE, SALTICIDAE) IN SOUTH CAROLINA¹

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ABSTRACT

Observations were made on the reproductive periods of nine species of *Phidippus* occurring in South Carolina. *Phidippus audax* (Hentz) oviposited from May through the following early spring, while most other species had much shorter and seasonally defined oviposition periods. The reproductive periods noted in these studies were similar to published reports from other regions where these species occur.

INTRODUCTION

The occurrence of *Phidippus* spp. in South Carolina has been reported by Roach and Edwards (1984) and Gaddy and Morse (1985). Many of these species occur in the same habitats and are often difficult to separate taxonomically. The use of genetic product analyses to identify and to study the phylogenetic relationships of many of the species that occur in the southeastern United States was reported by Terranova and Roach (1987a, 1987b). Because the immatures of several species may compete for habitat and prey concurrently, it is important to know the seasonal phenology of each species. Most studies of *Phidippus* spp. reproduction cycles in the literature are limited to observations on the egg sacs of individuals or a limited number of species in a geographical region. These studies were reviewed by Edwards (1980) who also reported his observations on the reproductive cycles and egg masses of *Phidippus* spp. occurring in Florida. In this report, I present a summary of seven years of observations on the reproductive periods of nine of the eleven *Phidippus* spp. occurring in South Carolina and compare these periods to those reported from other parts of each species range.

METHODS

During the course of collecting salticids for other studies (Roach 1983; Roach & Edwards 1984; Terranova & Roach 1987a,b), numerous specimens of *Phidippus* spp. were captured and held for observation. Collection methods

¹In cooperation with the South Carolina Agricultural Experiment Station. This article reports the results of research only. Mention of a proprietary product does not constitute endorsement or a recommendation for its use by the USDA.

varied according to habitat being sampled, but were primarily by sweep-net sampling and visual searching. Spiders thus collected were placed in clear plastic containers (8×8 or 8×4 cm) and held in a programmed environmental cabinet at $27 \pm 2^\circ\text{C}$, RH $50 \pm 10\%$, and a photoperiod of 14:10 (L:D). Spiders were fed *Heliothis* spp. larvae approximately the same size as the spider every 2 to 3 days until the natural death of the spiders. Observations on egg sac production included in this report are from gravid females collected in the wild.

RESULTS

The most commonly collected species of *Phidippus* in field habitats in South Carolina is *P. audax* (Hentz). This species began egg sac formation and oviposition in early May, and continued through most of the year (Table 1). Multiple egg sacs by *P. audax* were common, with an average of 2.75 per female. Table 2 shows the number of eggs per sac and the relative periods of their occurrence. In these observations, the mean number of eggs per sac (60) was about equal for all except possibly the sixth, even though the range (15-164) of eggs per sac was quite variable.

Phidippus clarus Keyserling was most frequently collected from old field habitats and lakeshore areas, and generally shared the same habitats as *P. audax*. However, the seasonal reproductive cycle of *P. clarus* was more restricted than *P. audax* (Table 1). *P. clarus* females oviposited during August and September and spiderlings dispersed from September through January.

Another species that occupied habitats similar to *P. clarus* and *P. audax* was *P. princeps* (Peckham & Peckham). However, it was only found in old field habitats, particularly in wooded areas, and on young pines in reforested areas. This species was common, but less generally distributed than *P. clarus* over the areas sampled. Only two gravid females were observed in this study. During the period from February to April, one produced a single egg sac and the other produced two egg sacs. The average number of eggs per sac (32) was considerably less than that of the previous two species.

Phidippus mystaceus (Hentz) has been collected only from the western foothills of South Carolina. Two gravid females included in this study were collected with egg sacs on 28 February and 23 March in Pickens County, SC by J. Brushwein. Each female produced only one egg sac, one with 76 and the other with 92 eggs (Table 1). Spiderlings from both egg sacs dispersed during mid April. Collection records from Pickens County indicated this species is found on shrubs, trees, and on the ground under protective coverings.

Phidippus otiosus (Hentz) was collected state-wide and is primarily an arboreal species. This species matured during the fall and produced egg sacs from December to February (Table 1).

Phidippus whitmani Peckham & Peckham was also collected statewide exclusively from woods litter, primarily in older, mixed hardwood areas. Of six females observed, oviposition occurred in July and August, and no female produced more than one egg sac (Table 1).

The remaining species included in this report (Table 1) were rarely collected and thus observations on these species are limited. *Phidippus putnami* (Peckham & Peckham) adults were collected from low limbs on the edge of mixed

Table 1.—Oviposition periods, fecundity, and spiderling dispersal of *Phidippus* species in South Carolina. *—Spiderlings dispersing when found so number may possibly be lower than normal. **—Not counted; dispersal observed.

| Species | Number observed | Oviposition period | \bar{X} Egg sac/ female | Range of egg sac/female | \bar{X} Eggs /egg sac | Range of eggs/egg sac | \bar{X} Total eggs/female | Spiderling dispersal period |
|----------------------|--------------------|-----------------------|------------------------------|----------------------------|----------------------------|--------------------------|--------------------------------|--------------------------------|
| <i>P. audax</i> | 11 | May-Mar. | 2.75 | 1-6 | 64.0 | 15-164 | 192 | 4 June-3 Mar. |
| <i>P. clarus</i> | 6 | Aug.-Sept. | 1.7 | 1-3 | 83.3 | 7-207 | 150 | 23 Sept.-25 Jan. |
| <i>P. princeps</i> | 2 | Feb.-Apr. | 1.5 | 1-2 | 32.0 | 21-60 | 48 | 9 Mar.-10 July |
| <i>P. mystaceus</i> | 2 | Feb.-Mar. | 1 | 1 | 84.0 | 76-92 | 84 | 14 Apr.-18 Apr. |
| <i>P. otiosus</i> | 3 | Dec.-Feb. | 1.3 | 1-2 | 101.0 | 19-150 | 135 | 21 Jan.-13 Feb. |
| <i>P. putnami</i> | 1 | Oct. | 1 | 1 | 47* | 47* | 47* | Oct. |
| <i>P. regius</i> | 1 | Jan. | 1 | 1 | 138 | 138 | 138 | 23 Feb. |
| <i>P. whitmani</i> | 6 | July-Aug. | 1 | 1 | 43.3 | 19-62 | 43.3 | 5 Sept.-16 Nov. |
| <i>P. cardinalis</i> | 2 | Mar.-Apr. | 1 | 1 | NC** | - | NC** | April-May |

Table 2.—Observations on *Phidippus audax* egg sacs and the periods of spiderling dispersal in eastern South Carolina. Numbers in parentheses indicate number of egg masses observed.

| Observation | Egg sacs | | | | | |
|--|----------------|-----------------|-----------------|-----------------|-----------------|--------|
| | 1st | 2nd | 3rd | 4th | 5th | 6th |
| \bar{X} Spiderlings per egg sac | 71(11) | 68(9) | 54(5) | 68(4) | 67(2) | 31(1) |
| Range of spiderlings/egg sac | 31-164 | 15-127 | 31-67 | 47-97 | 46-88 | 31 |
| \bar{X} Date of spiderling dispersal | 27 June | 6 Aug. | 3 Sept. | 30 Sept. | 23 Oct. | 3 Mar. |
| Range of spiderling dispersal dates | 4 June-14 July | 15 July-27 Aug. | 7 Aug.-11 Sept. | 26 Sept.-8 Oct. | 23 Oct.-15 Nov. | Mar. |

hardwood areas during late summer and early fall. Only one gravid female was collected with an egg sac and the spiderlings were possibly dispersing when found. This female did not produce another egg sac before dying in December.

Phidippus regius C. L. Koch was collected only in coastal areas, and again only one gravid female was observed. It was collected in November and produced one egg sac in February (Table 1).

Phidippus cardinalis (Hentz) was collected only in the foothills area of the state by J. Brushwein. He collected two females with egg sacs in March and April, 1986, but unfortunately did not count the number of eggs per sac.

DISCUSSION

Phidippus audax occurs widely over most of the United States and several reports of seasonal occurrence are available. Gibson (1947), in Tennessee, reported that *P. audax* overwintered as immatures and adults but did not deposit eggs until July. Kaston (1981) indicated that adults matured in late April to early May in Connecticut and laid eggs in June and July, with single females constructing up to three egg sacs. Snetsinger (1955), in Illinois, reported that *P. audax* mated in May and June and deposited eggs in June and July. Edwards (1980) indicated a maturation period primarily in May and June for Florida. Taylor & Peck (1975) compared southern Texas and northern Missouri forms of *P. audax*, and indicated a spring maturation period with up to six egg sacs per female, averaging 41.7 to 85.5 young per egg sac. They also found that later egg sacs for each female contained fewer young than earlier deposited egg sacs. These results are similar to those found in the present study except that egg sacs deposited successively did not contain fewer eggs than those produced earlier, with the possible exception of the sixth egg sac.

Oviposition, by *P. clarus* was observed in August-September in South Carolina. Kaston (1981), in Connecticut, reported mating of *P. clarus* in June and observation of an egg sac in late July; he also indicated a *P. clarus* female was collected on 31 August while guarding an egg sac with 47 eggs. Snetsinger (1955) observed mating of *P. clarus* in Illinois from late June to early August and egg sac formation August to October. Edwards (1980) reported *P. clarus* matured in July and August in Florida. Although there is variability in maturation in this species, egg sac formation occurs primarily from late July to October in the geographic area from Florida to Illinois.

Kaston (1981) reported that *P. princeps* matured in April and May in Connecticut and laid eggs as early as May; he also reported collecting a female guarding eggs on 10 June. Cutler (1965), in New York, reported seeing adults in September. In Florida, *P. princeps* is uncommon, but Edwards (1980) stated that the oviposition period was from May to July. All of these periods are somewhat later than the February-April oviposition period noted in South Carolina.

Berry (1970) reported collecting a single adult of *P. mystaceus* in June in the Piedmont region of North Carolina. Kelley (1979) collected several mature specimens in Pickens County, SC, and indicated the breeding season is from April to May in that area. Edwards (1980) indicated the oviposition period of *P. mystaceus* in northern Florida is October through May. Kaston (1981) indicated that this species is rare in Connecticut. Present observations on spiders collected

in Pickens County, SC indicated that oviposition by *P. mystaceus* occurs in February and March. Thus, in its eastern range, *P. mystaceus* apparently matures during the fall and winter and breeds during spring and early summer.

Phidippus otiosus (also known as *P. pulcher*) is primarily a Southeastern species and the only extensive phenology of this species reported in the literature is by Edwards (1980) for northern Florida. He indicated this species matures from September to November and oviposits from January to June. In South Carolina, this species matured in the fall and the collected females oviposited from December through February.

The only information found in the literature on the reproductive cycle of *P. putnami* is for northern Florida (Edwards 1980). He reported that this species matured in July and August, and oviposited from August through October. The collection of adults in late summer and early fall, along with the collection of an egg sac in October, indicate a similar cycle in South Carolina.

Phidippus regius is primarily a southeastern species which matures during September and October and oviposits from October to June in Florida (Edwards 1980). My observations indicate a similar cycle for *P. regius* in the coastal area of South Carolina.

Phidippus whitmani is a widely distributed species that matures in May in Connecticut (Kaston 1981), June in North Carolina (Berry 1970), and May or June in Florida (Edwards 1980). In South Carolina, the pattern is similar, with adults collected during the summer and oviposition observed during July and August.

Kaston (1981) reported that *P. cardinalis* adults were collected in Connecticut from late May to October, while Edwards (1980) indicated that in Florida the species matures from September to November and oviposits February through May. *Phidippus cardinalis* was only collected with egg sacs during March and April in South Carolina and apparently is not a common species over most of the state. Thus, this species may have a somewhat later maturity period in its more northern range.

Two other *Phidippus* species, *P. apacheanus* Chamberlin & Gertsch and *P. purpuratus* Keyserling, also occur in South Carolina but no adult females have been collected and observed so their phenology in the region is unknown. However, Edwards (1980) indicated that *P. apacheanus* matured in September-October in northern Florida, while Gardner (1965) reported that the species matured during the same period in the area around Reno, Nevada. *Phidippus purpuratus* is more common in the northeastern states and adults occur from May-September in Connecticut (Kaston 1981).

In summary, the reproductive periods of the various *Phidippus* species vary in time of occurrence and possibly in other phenological parameters. The information found in the report should be useful in predicting what stage of each species will be present in various habitats during certain periods of the year.

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THE SPIDER GENUS *CYBAEOTA* (ARANEAE, AGELENIDAE)

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ABSTRACT

Cybaeota Chamberlin and Ivie, 1933 (a genus of small, Nearctic, woodland spiders) is revised to include four species: *Cybaeota calcarata*, the type species, was described by Emerton in 1911, and *C. nana*, *C. munda*, and *C. shastae* were described by Chamberlin and Ivie in 1937. *Cybaeota concolor* Chamberlin and Ivie, 1937 is synonymized under *C. nana*. *Cybaeota vancouverana* and *C. wasatchensis* (both of Chamberlin and Ivie, 1937) are synonymized under *C. shastae*. The relationship of *Cybaeota* to other Cybaeinae is discussed.

INTRODUCTION

In 1911 J. H. Emerton described what is now the type species of *Cybaeota* as *Liocranum calcaratum*. He placed it in the Clubionidae, apparently because of the similarity of this cryptic, eastern North American species to certain clubionid spiders (e.g., *Scotinella* Banks) in size and the possession of conspicuous pairs of ventral macrosetae on various leg segments. Some years later R. V. Chamberlin and W. Ivie (1933), citing the presence of an unpaired third tarsal claw and the general similarity of the male palpus to that of *Cybaeus* L. Koch, transferred this species to the Agelenidae and placed it in a new genus *Cybaeota*. Since 1933 *Cybaeota* usually has been considered a member of the subfamily Cybaeinae (currently considered to encompass the genera *Cybaeina*, *Cybaeota*, and *Cybaeozyga* of Chamberlin and Ivie, and *Cybaeus*) of the Agelenidae (Roewer 1954; Bonnet 1956; but see Lehtinen 1967 and Brignoli 1983).

Subsequently Chamberlin and Ivie (1937) described *C. concolor*, *C. munda*, *C. nana*, *C. shastae*, *C. vancouverana* and *C. wasatchensis* from about a dozen specimens collected from British Columbia, California, and Utah. These species were diagnosed on the basis of abdominal pigmentation variations and small genitalic differences. As is often found in the taxonomic work of Chamberlin (in particular) and Ivie the descriptions are terse and vague and the drawings difficult to interpret for specimen identification. The present paper is the first in a series planned to sort out the general tangle of cybaeine systematics and test the hypothesis of cybaeine monophyly.

Cybaeota is a distinct grouping and is probably monophyletic. Genitalic apomorphies of the genus are: (1) the structure of the retrolateral tibial apophyses and the position of the bristly seta between them (Fig. 17), and (2) the structure and placement of the spermathecae and connecting ducts (Figs. 25, 28, 38).

The putative monophyly of the taxon Cybaeinae including *Cybaeota* is less well-supported. The similarities in the general structure of the male palpus shared by *Cybaeota* and *Cybaeus* are also seen in other, more distantly related genera such as *Altella* and *Devade* (both of Simon) in the Dictynidae, or *Cicurina* Menge and *Tegenaria* Latreille in the Agelenidae. *Cybaeota* strongly resembles *Cybaeina* in the arrangement of the ventral tibial and metatarsal macrosetae (Fig. 9) and in the fine structure of their sockets (Fig. 10), but these characters are also seen in various clubionid genera (e.g., *Scotinella* as mentioned above) and some other divergent agelenids (e.g., *Ethobuella* Chamberlin and Ivie and *Cicurina*) as well as in *Liocranoides* Keyserling (Tengellidae) and *Ischnothyreus* Simon (Oonopidae). These characters are probably present in combination in other genera as well. Conspicuous, paired, ventral tibial macrosetae are of widespread but scattered distribution amongst spiders and the socket reinforcements are present in all genera possessing such macrosetae of which I had specimens to study (i.e., those listed above). The intriguing distribution of these characters suggests that they are homoplasies (or perhaps shared plesiomorphies) and probably are not indicators of close relationship. Although no good synapomorphies can be found to support the inclusion of *Cybaeota* in the Cybaeinae, neither have any been found which demonstrate a closer relationship of *Cybaeota* to any other taxa. *Cybaeota* is therefore left in the Cybaeinae.

In this revision three new synonyms are proposed, reducing the number of recognized species of *Cybaeota* from "seven species described and several others known" (Roth and Brame 1972) to four. *Cybaeota concolor* is synonymized under *C. nana*; and *C. wasatchensis* and *C. vancouverana* under *C. shastae*. The collecting activities of V. D. Roth and W. J. Gertsch have been largely responsible for boosting the number of *Cybaeota* specimens available for study. Because of this increase, pigmentation differences used by Chamberlin and Ivie to delimit various species can be seen to be clinal variations within species.

This revision has resulted from the study of about 350 specimens from my personal collection (RGB) or kindly lent by the following institutions and individuals: the American Museum of Natural History (AMNH), Dr. N. I. Platnick; the California Academy of Sciences (CAS), Dr. W. J. Pulawski; the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC), Dr. C. D. Dondale; the Museum of Comparative Zoology (MCZ), Dr. H. W. Levi; Dr. Robin E. Leech (REL); and Mr. Vincent D. Roth (VDR).

Methods.—Specimens were examined and measured under a stereo dissecting microscope with an ocular micrometer reticle attached. Measurements are accurate to 0.01 mm. Identifications were made through the examination of male and female genitalia (dissected from the spiders and cleared in clove oil) under a compound microscope. The small size of these spiders makes identification with a dissecting microscope difficult. Drawings were made either with the aid of a drawing tube attached to the compound microscope or a squared grid reticle in one eyepiece of the dissecting microscope. Scanning electron micrographs were made with a Hitachi S-570 SEM.

Abbreviations used in text are as follows: CL, CW (carapace length and width); SL, SW (sternum length and width). Other abbreviations are explained in figure legends. Standard postal abbreviations are used for states and provinces. Statistics are presented as sample range (mean \pm standard deviation). Measurements are in millimeters.

Genus *Cybaeota* Chamberlin and Ivie

Liocranum (in part): Emerton, 1911:402, Plate V, figs. 4, 4a-f.

Cybaeota Chamberlin and Ivie, 1933:3, figs. 1-10, type species *Liocranum calcaratum* Emerton, 1911, by monotypy; Chamberlin and Ivie, 1937:226, figs. 68-84; Roewer, 1954:87; Bonnet, 1956:1298; Lehtinen, 1967:226; Roth and Brame, 1972:17, figs. 5, 23-24; Brignoli, 1983:483; Roth and Brown, 1986:3.

Diagnosis.—Male with characteristic distal and medial retrolateral tibial apophyses, with single bristly seta located between them (Fig. 17); female with simple genitalia, copulatory opening single, with two, short connecting ducts each leading to single, large, circular, heavily sclerotized spermatheca (Figs. 25, 28, 38).

Description.—Small spiders, with carapace lengths averaging 0.74 (male) to 1.08 mm (female); females usually slightly larger than males. Carapace (Figs. 1, 3) darkly pigmented around eyes, pale yellow elsewhere, longer than wide, glabrous except for small number of setae along midline and around eyes; dorsal groove short, longitudinal. Usually eight eyes (Figs. 1, 3) in two rows (one specimen of *C. shastae* known with posterior median eyes missing); posterior row longer than anterior; both rows slightly recurved in dorsal view; in frontal view anterior row straight, posterior row recurved; anterior median eyes reduced; anterior laterals largest; posteriors subequal, somewhat smaller than anterior laterals; median ocular quadrangle widest posteriorly, about twice height of clypeus. Promargin of cheliceral fang furrow with three subequal teeth (Fig. 3), retromargin with two to five small teeth.

Sternum (Fig. 2) shield-shaped, extending posteriorly short distance between coxae IV, nearly as wide as long, pale yellow, lightly clothed with fine setae. Labium (Fig. 2) short, wider than long. Serrula (Fig. 16) well developed.

Legs pale yellow, without markings; I and IV longest, subequal, III shortest; I and II conspicuously setose, femur I with two (occasionally 1) distal prolateral macrosetae, other macrosetae ventral, tibia I 2-2-2-2-2, metatarsus I 2-2-2, tibia II 2-2-2-2-1, metatarsus II 2-2-1, tibia III 1-2-1; all tibial and metatarsal macrosetal sockets reinforced (as in Fig. 10). Each tarsus and metatarsus usually with two trichobothria dorsally (Fig. 13), arranged as in typical agelenids, with distal one longer than proximal. Trichobothrial sockets and tarsal organs typically araneomorph (Figs. 14, 15).

Abdomen (Figs. 1, 2) rounded, unornamented, concolorous to strongly patterned (variable within species, Figs. 6-8), lightly clothed with fine setae; spiracle (Figs. 2, 11) just anterior to and as wide as colulus, which is represented by two setae; anterior spinnerets (Figs. 2, 12) broad, separated by about width of colulus, as long as posterior spinnerets; posterior spinnerets narrow, separated by width of anal tubercle; median spinnerets small, contiguous; apical segments of all spinnerets subequal, much shorter than basal segments.

Epigynum simple, externally marked by transverse (Fig. 25) or inverted "U-shaped" (Fig. 27) copulatory opening; shape and position of spermathecae and connecting ducts usually discernible through integument (Figs. 2, 30-34); bursa a shallow pocket (Fig. 25) or nearly absent; connecting ducts short, sinuous (most noticeably in anterior or posterior view), separately joined to anterior margin of bursa (Fig. 25) or to anterolateral (Figs. 36, 37) or posterolateral (Fig. 27) margins of copulatory opening when bursa reduced; spermathecae simple, large,

rounded, heavily sclerotized, contiguous (Figs. 25, 26) or moderately separated; single fertilization duct exiting each spermatheca posteriorly (Fig. 27).

Male pedipalp (see Fig. 4 for view of expanded palpal organ) simple, without patellar apophyses, with distal and medial retrolateral tibial apophyses uniform among species (Fig. 17); basal haematodocha well-developed (with petiole apparently incorporated onto proximal surface), merging with narrow ringlike subtegulum; subtegulum connected to broad, rounded tegulum by inconspicuous middle haematodocha; embolus short, stout, continuous with surface of tegulum (Fig. 19) (Gering [1953] incorrectly described the embolus of *Cybaeota* as terminating in a long filament such as in *Wadotes* Chamberlin; see Bennett 1987); conductor (Figs. 21, 22) flexibly attached (by distal haematodocha?) to surface of tegulum, with broad, shallowly excavated plate dorsal to tip of embolus, with two arms, prolateral arm varying according to species, retrolateral arm dagger-shaped; receptaculum seminis (Fig. 5) visible in palpi cleared in clove oil, well-sclerotized throughout, coiled through $\sim 540^\circ$, fundus "s-shaped", lying deep within subtegulum, reservoir in close association with outer margin of tegulum through $\sim 360^\circ$, ejaculatory duct "s-shaped" at base of embolus, opening just proximal to embolus tip.

Natural history notes.—The orientation of palpal sclerites on the partially expanded palpus of one male *C. nana* (Fig. 18) suggests a functional relationship between the retrolateral arm of the conductor and the medial retrolateral tibial apophysis. During inflation of the basal haematodocha the conductor is forced proximally along the tibia until the retrolateral arm of the conductor and the medial retrolateral tibial apophysis engage. This action should impart some amount of rigidity to the cymbium as the embolus is inserted into the epigynum.

The cryptic nature of all species of *Cybaeota* is probably responsible for their rare appearance in collections. However, within particular microhabitats, species of this genus may be dominant members of the arthropod community as has been demonstrated for other "rare" organisms (e.g., see Bennett 1985 and discussion under *C. shastae*).

The tiny spiders of this genus are found in leaf litter, moss on tree trunks, and other debris on the floor of Nearctic forests. The species are concentrated in western North America from Utah west to California and coastally north to Alaska (Figs. 40-42). One species occurs in the northeastern United States and adjacent regions of Canada (Fig. 39).

KEY TO SPECIES OF *CYBAEOTA*

(Male of *C. munda* unknown)

1. Prolateral arm of conductor bifid (Fig. 19). Spermathecae large, nearly contiguous (Figs. 25, 26). NE. USA and adjacent areas of ON and PQ (Fig. 39).....*calcarata*
 Prolateral arm of conductor not bifid. Spermathecae smaller, separated by about one-half their diameter. W. North America.....2
2. Prolateral arm of conductor pointed and directed towards retrolateral arm (Figs. 21, 22). Connecting ducts joining copulatory opening posterolaterally (Figs. 27-29). AK to S. CA with (apparently) disjunct population in UT (Figs. 41, 42).....*shastae*

- Prolateral arm of conductor otherwise. Connecting ducts joining copulatory opening anterolaterally. Not known north of S. BC (Fig. 40).....3
3. Prolateral arm of conductor knob-like and directed ventrally (Figs. 23, 24). Connecting ducts not extending well into spermathecae in ventral view (Figs. 37, 38). Relatively small species (avg. female carapace length 0.8 mm). S. BC to S. CA and N. UT (Fig. 40).....*nana*
Male unknown. Connecting ducts extending well into spermathecae in ventral view (Figs. 35, 36). Relatively large species (avg. female carapace length 1.1 mm). S. OR and mid-coastal CA (Fig. 40).....*munda*

Cybaeota calcarata (Emerton)

Figs. 19, 20, 25, 26, 30, 39

Liocranum calcaratum Emerton, 1911:402, Plate V, figs. 4, 4a-f.

C. calcarata: Chamberlin and Ivie 1933:4, figs. 1-10; Roewer 1954:87; Bonnet 1956:1298; Roth and Brown 1986:3.

C. calcaratum: Kaston 1976:37, figs. 31-32.

Diagnosis.—Male with bifid tip on prolateral arm of conductor (Fig. 19). Female with relatively large, nearly contiguous spermathecae (Figs. 25-26).

Description.—As for genus. *Male*: $N=7$ including male syntype. CL $0.92-1.13$ (0.99 ± 0.07), CW $0.77-0.88$ (0.80 ± 0.04), SL $0.60-0.70$ (0.63 ± 0.04), SW $0.57-0.62$ (0.60 ± 0.02). Syntype CL 1.13, CW 0.88, SL 0.70, SW 0.62. Retrolateral arm of conductor with ventral longitudinal keel.

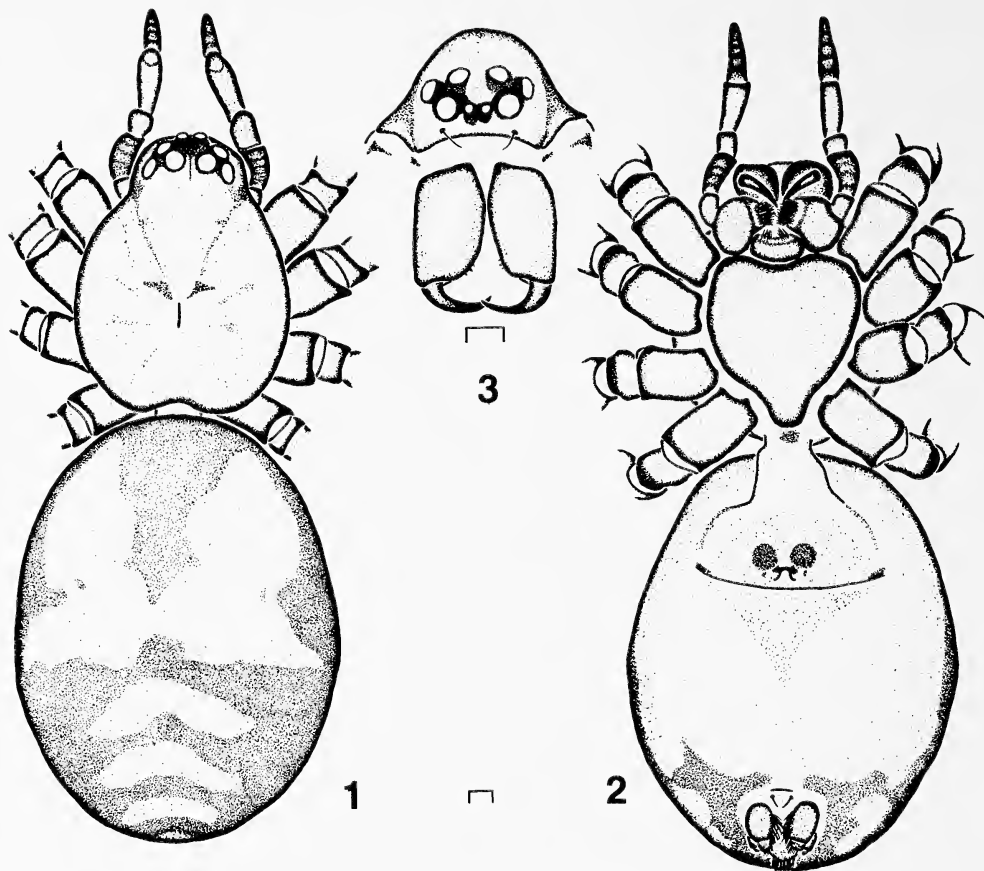
Female: $N=20$ including female syntype. CL $0.96-1.13$ (1.04 ± 0.04), CW $0.73-0.90$ (0.83 ± 0.04), SL $0.59-0.70$ (0.66 ± 0.03), SW $0.56-0.65$ (0.61 ± 0.02). Syntype CL 1.13, CW 0.87, SL 0.70, SW 0.62.

Distribution and natural history.—*Cybaeota calcarata* is the only species in this genus known from eastern North America (Fig. 39). It has been collected from forest floor litter and moss in widely scattered locales in Ontario, southern Quebec, Newfoundland, northern Michigan (Chickering 1935), New York, New Hampshire, and Massachusetts (Kaston 1948).

Collection evidence suggests a year-round presence of both sexes with mature males being common only in the summer.

Material examined.—*Type series*: two syntypes, NEW HAMPSHIRE; Coos Co., Great Gulf, Mt. Washington, 1 VIII 1910 (J. H. Emerton), 1 male, 1 female (MCZ). *Note*: Following Coddington (1986:4) I prefer, in this case, not to designate a lectotype and paralectotype from the syntypes.

CANADA: NF; Baie Verte Jct., 14 VIII 1984 (L. Hollett), 1 male (CNC), E of Daniels Hbr., 16 VIII 1984 (L. Hollett), 1 male, 1 female (CNC) 7 km S Pasadena, $49^{\circ}00'N/57^{\circ}36'W$, 17 VIII 1984 (L. Hollett), 1 female (CNC), Little Barachois Brook, 20 VIII 1984 (L. Hollett), 2 females (CNC), Caribou Lk., $48^{\circ}38'N/55^{\circ}01'W$, 24 IX 1984 (L. Hollett), 1 male (CNC), Crabbes R., $48^{\circ}13'N/58^{\circ}52'W$, 14 VIII 1985 (L. Hollett), 2 males, 1 female (CNC). ON; Algoma, Batchawana, 29 VII 1948 (W. Gertsch, W. Ivie, T. B. Kurata), 1 female (AMNH); Nipissing, Sproule Bay, Lk. Opeongo, Algonquin Pk., 26 VI-7 VII 1945 (W. Ivie, T. B. Kurata), 1 male, 4 females (AMNH), S Tea Lk., Algonquin Pk., 3-10 VII 1945 (W. Ivie, T. B. Kurata), 1 male, 1 female (AMNH), point W of Ko-Ko-Ko Bay, Lk. Temagami, 15-25 VIII 1948 (W. J. Gertsch, W. Ivie, T. B. Kurata), 1 male, 2 females (AMNH), Lk. Opeongo, Algonquin Pk., 17 VIII 1948 (W. J. Gertsch, T. B. Kurata), 1 male, 5 females (AMNH); Ottawa/Carleton, Kinburn, in pine duff, 8 IV 1962 (J. E. H. Martin), 1 male (CNC); Thunder Bay, 3 mi. NW Finmark, $N48:34/W89:50$, 23 VII 1965 (J. and W. Ivie), 1 female (AMNH). PQ; St. Hippolyte, 25 VI 1974 (M.-C. Tarrisants), 1 female (CNC). USA: NH; Cheshire, Mt. Monadnock, 13 VI 1947 (A. M. Chickering), 1 female (MCZ). NY; Albany, Rensselaerville, Huych Preserve, 8 VII



Figs. 1, 2.—*Cybaeota munda*, female, Pinnacles Nat. Mon. CA: 1, dorsal view; 2, ventral view. Fig. 3.—*Cybaeota nana*, female, Josephine Co. OR, face and chelicerae, frontal view. Scale markers = 0.1 mm.

1948 (Bishop), 1 female (AMNH); *Tompkins*, 1 male, 1 female (AMNH). NO LOCALE; AC 3222, #1425 (Horace Britcher), 1 female (AMNH).

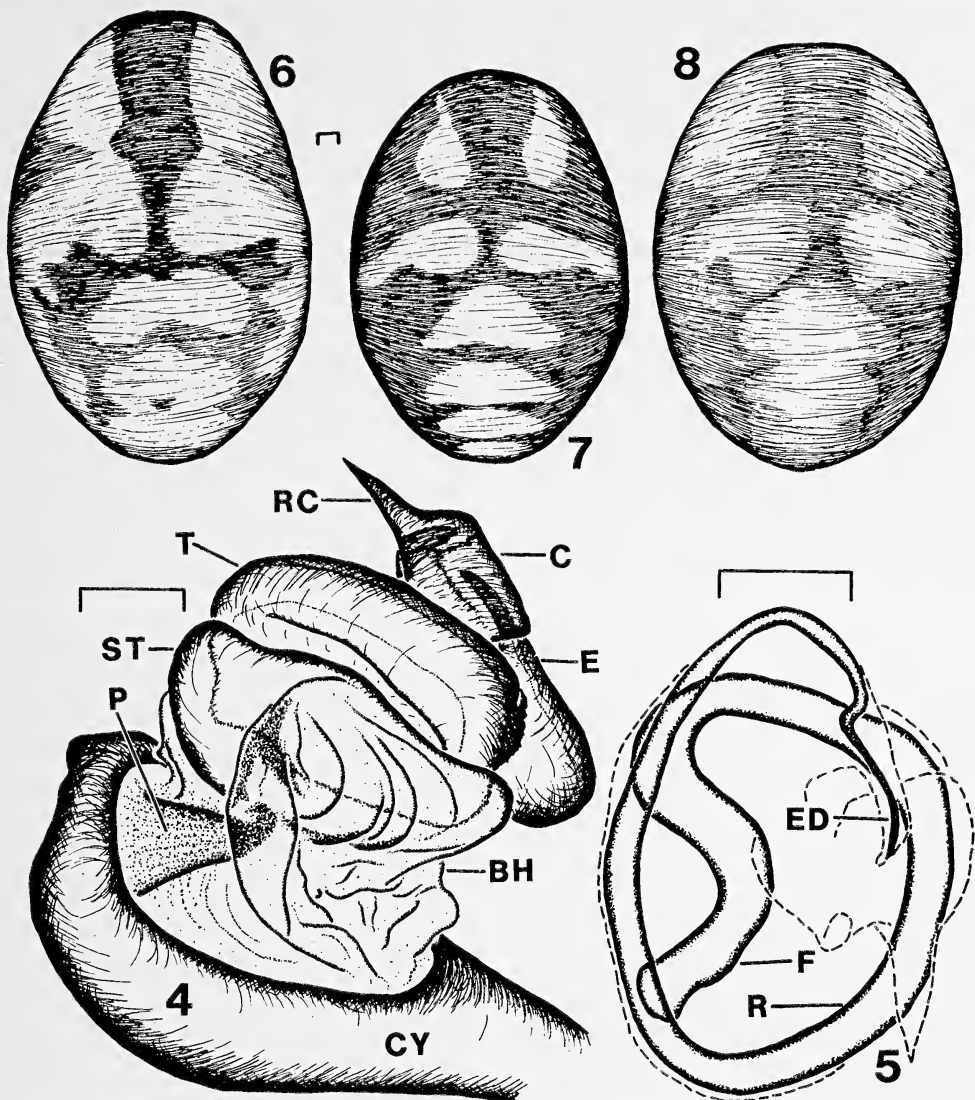
Cybaeota nana Chamberlin and Ivie
Figs. 3, 4-8, 18, 23, 24, 34, 37, 38, 40

Cybaeota concolor Chamberlin and Ivie, 1937:227, figs. 77, 78; Roewer 1954:87; Bonnet 1956:1298; Roth and Brown 1986:3. **NEW SYNONYMY**

C. nana Chamberlin and Ivie, 1937:229, figs. 74, 75, 79, 80; Roewer 1954:87; Bonnet 1956:1298; Roth and Brown 1986:3.

Diagnosis.—Male with retrolateral arm of conductor smoothly curved, ventrally directed, knob-like (Figs. 23, 24). Female with spermathecae separated by approximately one-half their diameter, and with connecting ducts joined to copulatory opening anterolaterally (Figs. 37, 38).

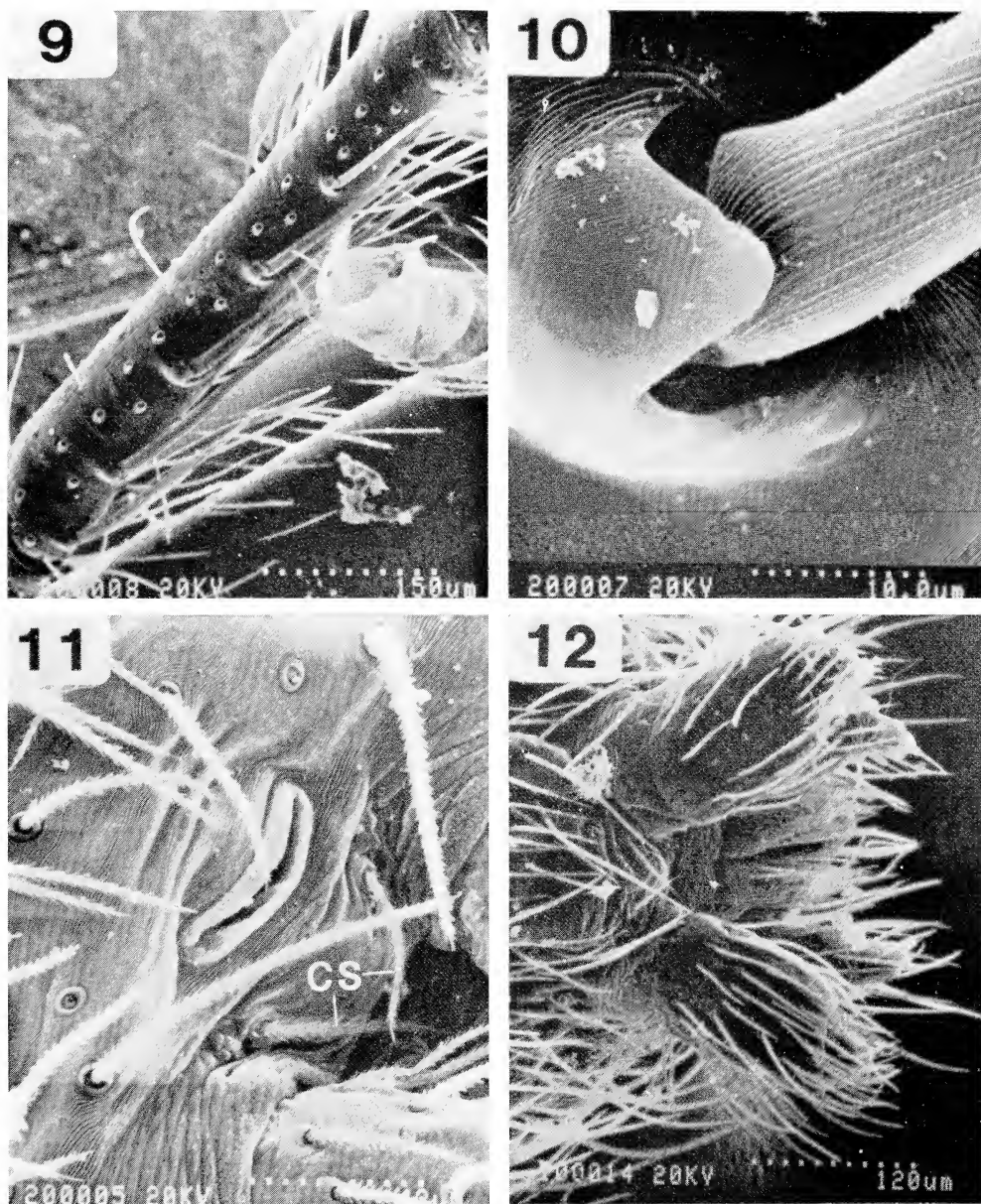
Description.—As for genus. *Male*: $N=21$ including holotype. CL 0.66-0.92 (0.75 ± 0.05), CW 0.55-0.73 (0.60 ± 0.04), SL 0.43-0.61 (0.49 ± 0.03), SW 0.43-0.53 (0.47 ± 0.02). Holotype CL 0.70, CW 0.55, SL 0.43, SW 0.43.



Figs. 4-8.—*Cybaeota nana*: 4, left male palpal tarsus with partially expanded genital bulb, retrolateral view; 5, receptaculum seminis of left genital bulb, ventral view, relative positions of conductor, embolus and tegulum indicated by dotted lines; 6-8, female abdomens, dorsal views indicating pattern variation within single population, Lost Lk. ID. Scale markers = 0.05 mm. BH=basal haematodocha, C=conductor, CY=cymbium, E=embolus, ED=ejaculatory duct, F=fundus, P=petiole, R=reservoir, RC=retrolateral arm of conductor, ST=subtegulum, T=tegulum.

Female: $N=44$ including holotype of *C. concolor*. CL 0.77-0.91 (0.83 ± 0.04), CW 0.60-0.73 (0.66 ± 0.03), SL 0.47-0.57 (0.53 ± 0.03), SW 0.46-0.55 (0.50 ± 0.02). Holotype of *C. concolor* CL 0.90, CW 0.74, SL 0.56, SW 0.53.

Distribution and natural history.—This species is known from extreme SW British Columbia south to S California with scattered inland records from E Washington, W Idaho, and N Utah (Fig. 40). *Cybaeota nana* appears to be absent from mid-coastal California. With the probable exception of the S California coast, *C. shastae* is sympatric with *C. nana* throughout the range of the latter.

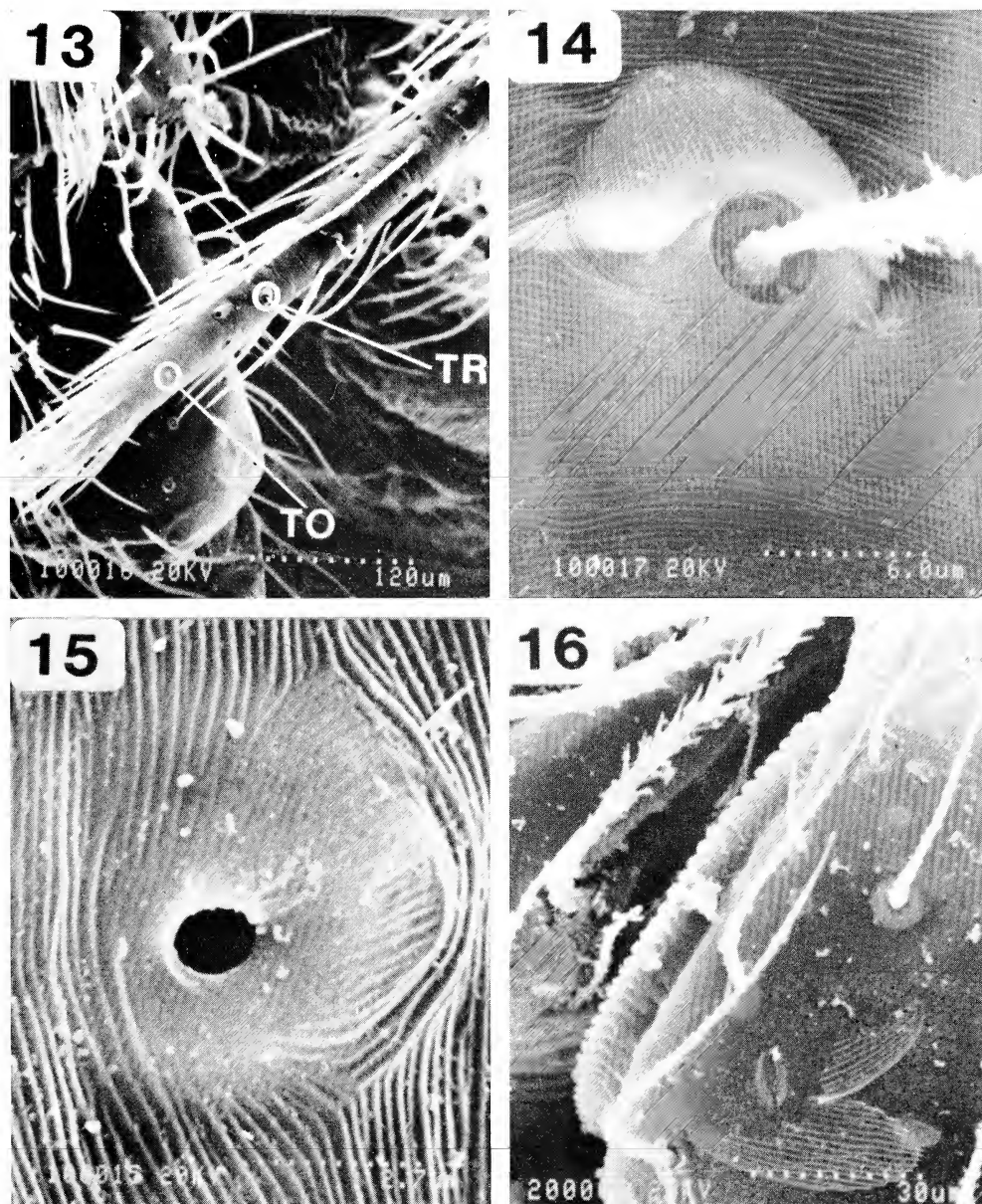


Figs. 9-11.—*Cybaeota shastae*, male, Victoria BC: 9, left tibia I, prolateral view; 10, same, macroseta base and socket; 11, colulus setae and spiracle, ventral view. Fig. 12.—*C. shastae*, female, Josephine Co. OR, spinnerets, ventral view. CS=colulus setae.

Specimens are usually taken from forest floor litter. At Corvallis, Oregon three females were found in a wood rat nest. Both sexes have been collected year-round but mature males are rarely collected in the first half of the year.

Notes on synonymy.—*Cybaeota concolor* has page precedence over *C. nana* but, if retained, the former name could lead to the erroneous supposition that this species is concolorous.

Chamberlin and Ivie (1937) named *C. nana* for a pair of spiders which they perceived as abdominal coloration variants of *C. shastae*. It is virtually impossible



Figs. 13-15.—*Cybaeota shastae*, female, Josephine Co. OR, tarsus IV: 13, dorsal view; 14, bothrium and hair; 15, tarsal organ. Fig. 16.—*C. shastae*, male, Victoria BC, serrula, right palpal endite, ventral view. TO=tarsal organ, TR=trichobothrial base.

non-arbitrarily to assign specimens of *Cybaeota* to any particular species on the basis of abdominal pattern and coloration. The genitalia of *C. nana* and *C. concolor* are identical and examination of all specimens with “nana/concolor”-like genitalia has shown a wide range of abdominal patterns. Groups of specimens from single collection locales (e.g., Cedar Lake, Stevens Co., WA; Lost Lake, ID; and City Creek, Salt Lake Co., UT) show great variability (Figs. 6-8), in one case from virtually concolorous to heavily patterned. There is a clinal trend observable across the range of this species: concolorous abdomens are

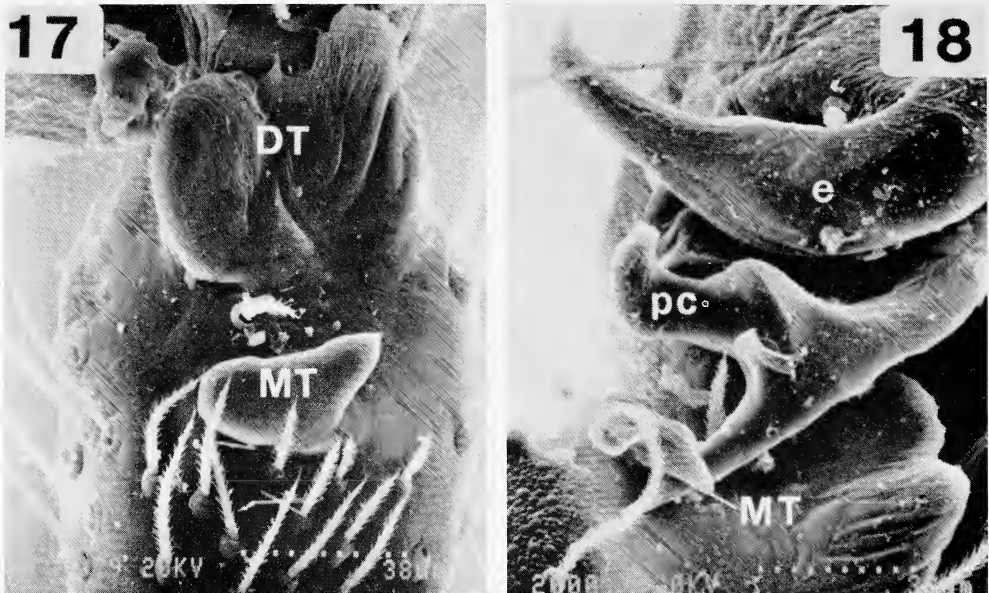
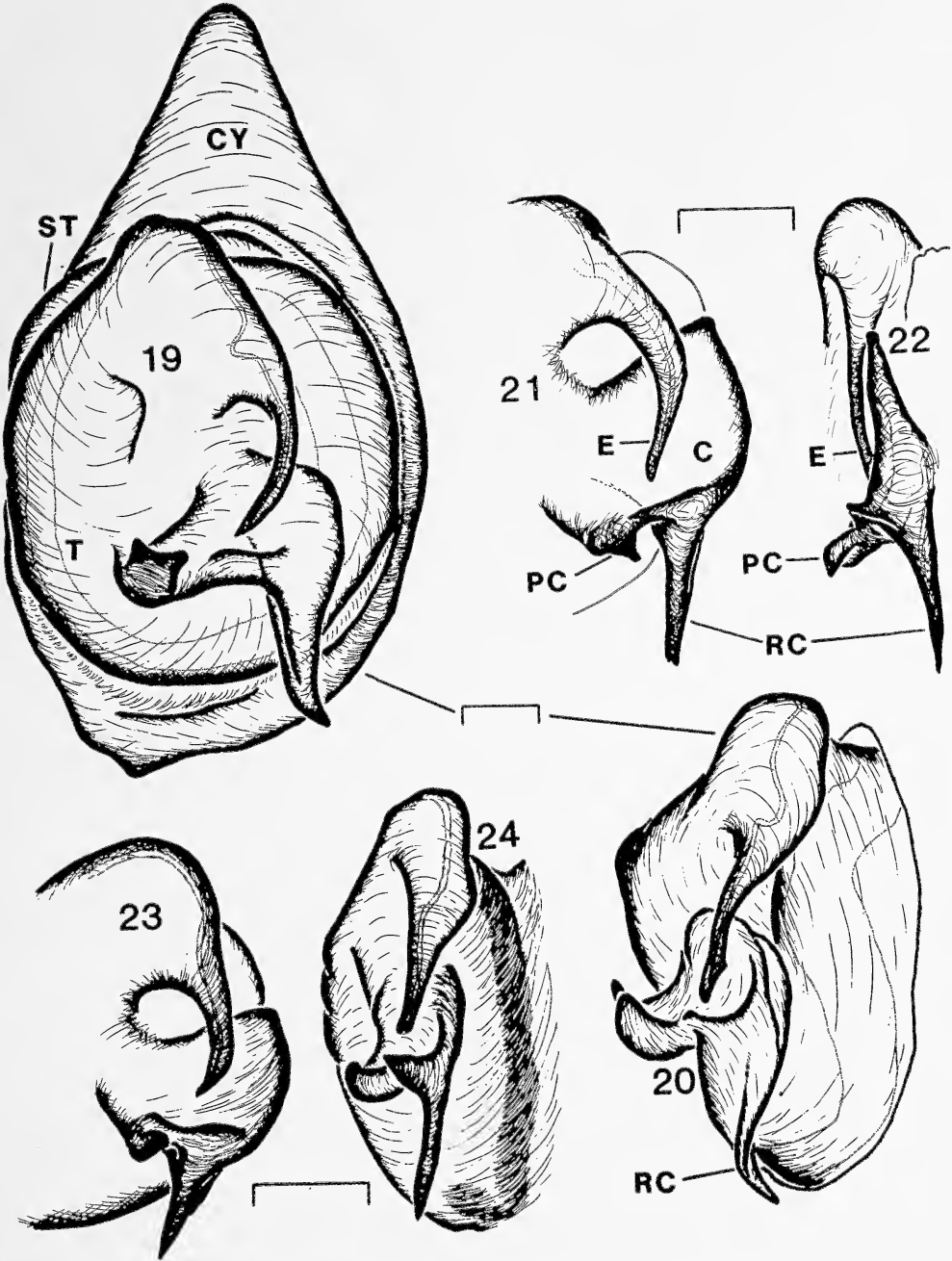


Fig. 17.—*Cybaeota shastae*, male, Josephine Co. OR, left palpal tibia, retrolateral view. Fig. 18.—*C. nana*, male, Los Angeles Co. CA, left palpal tibia and genital bulb, retrolateral view, showing interlocking of retrolateral arm of conductor with medial retrolateral tibial apophysis. DT, MT=distal and medial retrolateral tibial apophyses, PC=prolateral arm of conductor.

prevalent in the eastern part of the range (Utah), to the west abdominal patterns become more distinct and common as the coast is approached. (There is also an east-west clinal gradation in size: larger individuals are generally eastern—Utah females average CL 0.87 mm, coastal females average CL 0.81 mm.) The conformity of genitalia of specimens previously assigned to *C. nana* and *C. concolor* combined with the clinal variability in abdominal pigmentation justifies the synonymy of *C. concolor* under *C. nana*.

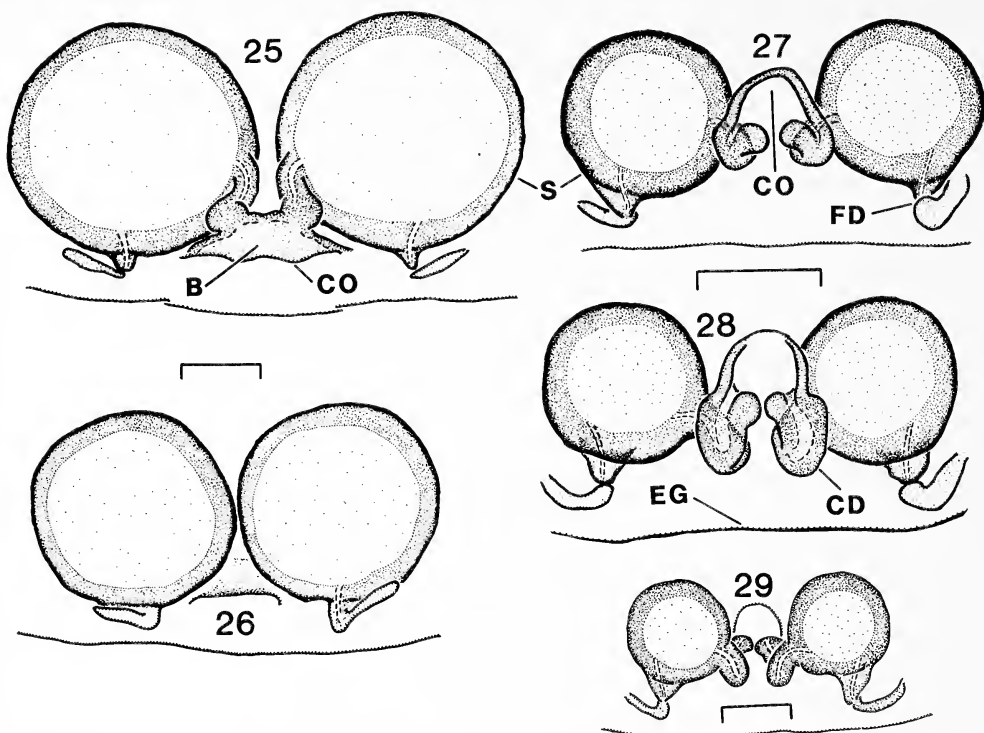
Material examined.—*Types*: Holotype of *C. nana*, BRITISH COLUMBIA; west side of Saanich Inlet, near Victoria, 14 IX 1935 (R. V. Chamberlin and W. Ivie), 1 male (and 1 allotype female) (AMNH). Holotype of *C. concolor*, UTAH; Salt Lake Co., Mill Creek Canyon, Wasatch Mtns., near Salt Lake City, no date (R. V. Chamberlin), 1 female (AMNH).

USA: CA; *Humboldt*, Carlotta, 15 IX 1961 (W. Ivie, W. Gertsch), 1 male, 1 female (AMNH); *Los Angeles*, Los Angeles Nat. For., 22 VI 1957 (I. Newell), 2 males, 3 females, 2 imm. (AMNH), 6 VII 1957 (I. Newell), 3 males, 3 females (AMNH); *Nevada*, Sardine Valley, 14 mi. NNE Truckee (A. Grigarick), 2 females, 1 imm. male (AMNH); *Riverside*, San Jacinto Mtns., VII 1952 (R. X. Schick), 1 female (AMNH); *Shasta*, Burney Falls, 18 VI 1954 (E. Schuster), 2 males, 2 females (AMNH); *Tulare*, 10 mi. W Johnsondale, 15 IX 1959 (W. Gertsch, V. Roth), 2 males, 1 female (AMNH); *Ventura*, summit Mt. Pinos, W of Lebec, 15 IX 1959 (W. Gertsch, V. Roth), 1 male, 6 females (AMNH). ID; Lost Lk., 27 VII 1939 (W. Ivie), 2 males, 5 females, 2 imm. (AMNH); *Adams*, Evergreen Camp, upper Weiser R., 17 X 1944, 4 females (AMNH). NE; *Washoe*, Hwy 27, 19 mi. SW Tahoe Jctn., 8420', 15 VIII 1968 (R. E. and A. V. Leech), 1 male (REL). OR; *Benton*, N of Corvallis, McDonald For., 3 XI 1949 (V. D. Roth), 1 female, 1 imm. (CAS), W of Corvallis, 44°33'N/123°22'W, 20 III 1937 (J. C. Chamberlin), 1 male, 1 female (AMNH), Corvallis, 24 IV 1949 (V. D. Roth), 1 female (CAS), 26 XI 1950 (V. D. Roth), 2 males, 6 females, 3 imm. (CAS), 21 V 1952 (Roth, Birge), 3 females (CAS), 9 mi. W Philomath, 29 VII 1953 (W. J. and J. W. Gertsch), 2 females (AMNH); *Josephine*, summit of Wolf Ck. Rd., 42°38'N/123°23'W, 12 V 1947 (I. M. Newell), 1 female (AMNH); *Marion*, Marion, 24 IV 1941 (J. C. Chamberlin), 1 male, 2 females (AMNH); *Washington*, Hillsboro, N45:30/W122:58, 1937 (J. C. Chamberlin), 2 females (AMNH). UT; *Daggett*, Rt. 44, 38 mi. N Vernal, 7200', 2 VIII 1959 (C. C. Hoff), 1 female (AMNH); *Salt Lake*, 3 mi. up City Ck. Cn., 40°47'N/



Figs. 19, 20.—*Cybaeota calcarata*, male syntype, Coos Co. NH, genital bulb: 19, ventral view including cymbium; 20, retrolateral view. Figs. 21, 22.—*C. shastae*, holotype male, Siskiyou Co. CA, conductor and embolus: 21, ventral view; 22, retrolateral view. Figs. 23, 24.—*C. nana*, male: 23, holotype, Saanich Inlet BC, conductor and embolus, ventral view; 24, "Redwoods" CA, genital bulb, retrolateral view. Scale markers=0.05 mm.

111°48'W, 25 VI 1962 (W. Ivie), 21 males, 8 females (AMNH), Mill Ck. Cn., 40°40'N/111°45'W, 1910-1925 (R. V. Chamberlin), 1 female (AMNH), 25 V 1924 (R. V. Chamberlin), 1 female (AMNH); *Utah*, Timpanogos Pk., American Fork Cn., 19 VIII 1941 (J. C. Chamberlin, W. Ivie), 1 female (AMNH). WA; *Kitsap*, N48/W123, 1 male (AMNH); *Pierce*, Tacoma, 9 VIII 1929 (R. V. Chamberlin), 1 female



Figs. 25, 26.—*Cybaeota calcarata*, cleared epigyna: 25, ventral view; 26, St. Hippolyte PQ, dorsal view. Figs. 27-29.—*C. shastae*, cleared epigyna: 27, Yosemite Nat. Pk., ventral view; 28, Weed CA, slightly posterior of ventral view; 29, same, dorsal view. Scale markers=0.05 mm. B=bursa, CD=connecting duct, CO=copulatory opening, EG=epigastric groove, FD=fertilization duct, S=spermatheca.

(AMNH); Stevens, 10 IX 1963 (J. and W. Ivie), 1 female, 1 imm. (AMNH), Cedar Lk., 48°45'N/117°36'W (J. and W. Ivie), 4 females (AMNH), 48°55'N/117°36'W, V 1962 (W. Ivie), 1 female (AMNH), 48°56'N/117°36'W, 30 IX 1964 (J. and W. Ivie), 5 females (AMNH).

Cybaeota munda Chamberlin and Ivie

Figs. 1, 2, 33, 35, 36, 40

Cybaeota munda Chamberlin and Ivie, 1937:228, figs. 83, 84; Roewer 1954:87; Bonnet 1956:1298; Roth and Brown 1986:3.

Diagnosis.—Male unknown. Female with connecting ducts intruding into spermathecae (Figs. 35, 36).

Description.—As for genus. *Female*: $N=4$. CL 1.01-1.17 (1.11), CW 0.81-0.92 (0.87), SL 0.62-0.75 (0.70), SW 0.59-0.65 (0.62). Holotype CL 1.13, CW 0.86, SL 0.68, SW 0.61.

Distribution.—*Cybaeota munda* has been collected near San Francisco and from southwestern Oregon (Fig. 40). It is the only *Cybaeota* species known from mid-coastal California. In Oregon, *C. munda* is sympatric with both *C. nana* and *C. shastae*.

Material examined.—*Holotype*: CALIFORNIA; San Mateo Co., La Honda, 1920-1921 (J. C. Chamberlin), 1 female (AMNH).

USA: CA; *San Benito*, Pinnacles Nat. Mon. (W. Gertsch, V. D. Roth), 1 female (AMNH). OR; *Douglas*, 5 mi. W Drain, 29 V 1948 (Roth, Brown), 1 female (CAS); *Josephine*, Grave Ck., 10 mi. E Placer, 22 VII 1962 (V. D. Roth), 1 female (CAS).

Cybaeota shastae Chamberlin and Ivie

Figs. 9-17, 21, 22, 27-29, 31, 32, 41, 42

Cybaeota shastae Chamberlin and Ivie, 1937:227, figs. 68-70; Roewer 1954:87; Bonnet 1956:1298; Roth and Brown 1986:3.

C. wasatchensis Chamberlin and Ivie, 1937:227, figs. 71-73, 76; Roewer 1954:88; Bonnet 1956:1298; Roth and Brown 1986:3. **NEW SYNONYMY**

C. vancouverana Chamberlin and Ivie, 1937:228, figs. 81, 82; Roewer 1954:87; Bonnet 1956:1298; Roth and Brown 1986:3. **NEW SYNONYMY**

Diagnosis.—Male with pointed prolateral arm of conductor deflected towards retrolateral arm (Figs. 21, 22). Female with spermathecae separated by about one-half their diameter, connecting ducts attached to posterolateral margins of copulatory opening (Figs. 27-29).

Description.—As for genus. *Male*: $N=24$ including holotypes of *C. shastae* and *C. wasatchensis*. CL 0.81-0.96 (0.87 ± 0.04), CW 0.62-0.78 (0.68 ± 0.04), SL 0.53-0.62 (0.57 ± 0.02), SW 0.48-0.59 (0.52 ± 0.03). Holotype CL 0.81, CW 0.64, SL 0.55, SW 0.52. Holotype of *C. wasatchensis* CL 0.94, CW 0.78, SL 0.61, SW 0.59.

Female: $N=61$ including holotype of *C. vancouverana*. CL 0.86-1.09 (0.92 ± 0.06), CW 0.65-0.87 (0.72 ± 0.05), SL 0.55-0.73 (0.59 ± 0.03), SW 0.51-0.65 (0.55 ± 0.03). Holotype of *C. vancouverana* CL 0.87, CW 0.68, SL 0.57, SW 0.52.

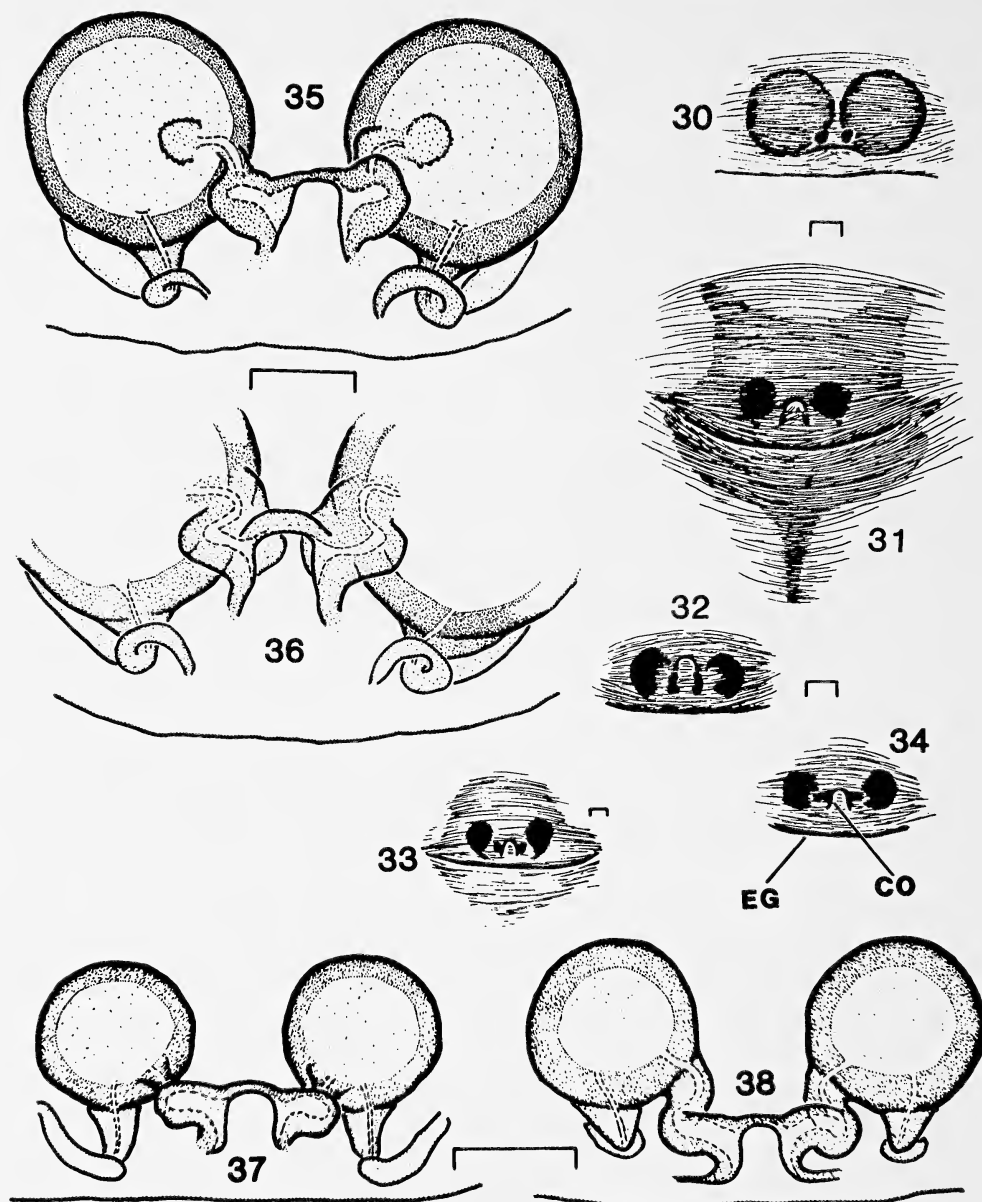
One male (CA; Shasta Co., Lassen Pk., 19 IX 1961) lacks posterior median eyes.

Distribution and natural history.—This is the most commonly collected species of *Cybaeota*. It is known from scattered locales along the Alaska panhandle, on Vancouver Island (British Columbia), and the Olympic Peninsula of Washington (Fig. 42). South from Washington, this species is found along the coast and inland to N California and south through the Sierra Nevada to S California (Fig. 41). A possibly disjunct population is known from the vicinity of Salt Lake City, Utah. *Cybaeota nana* is sympatric with *C. shastae* from S Vancouver Island southwards throughout the range of the latter.

Cybaeota shastae is probably common all along the British Columbia and Alaska panhandle coastlines. Berlese funnels produced good samples of this species (as well as other "rare" spiders such as *Ethobuella tuonops*) from moss taken from the trunks of red alder (*Alnus rubra* Bong.) and broadleaf maple (*Acer macrophyllum* Pursh) on S Vancouver Island. Mossy red alders are common along the BC and Alaska panhandle coasts. *Cybaeota shastae* was the most numerous spider in these Berlese samples.

Both sexes have been collected throughout the year. However, mature males are common only in late summer and fall. Mature males apparently appear earlier in more northerly parts of the species' range.

Notes on synonymy.—The three names *C. shastae*, *C. wasatchensis*, and *C. vancouverana* all refer to specific locales where each putative species was found. As there is no other reason to prefer one name over the others, *C. shastae* is



Figs. 30-34.—*Cybaeota*, uncleared epigyna, ventral views: 30, *C. calcarata*, St. Hippolyte PQ; 31, *C. shastae* with “vancouverana”-type pattern, Victoria BC; 32, *C. shastae* with no pattern, Weed CA; 33, holotype of *C. munda* with vestige of “vancouverana”-type pattern, La Honda CA; 34, *C. nana*, Stevens Co. WA. Figs. 35, 36.—*C. munda*, cleared epigyna, ventral views: 35, holotype, La Honda CA; 36, Josephine Co. OR. Figs. 37, 38.—*C. nana*, cleared epigyna, ventral views: 37, Lost Lk. ID; 38, Tacoma WA. Scale markers=0.05 mm.

chosen as senior synonym because of its page precedence. These new synonyms are here established for the same reasons as discussed under *C. nana*.

Variability from nearly concolorous to strongly patterned abdomens is seen in groups of specimens from Echo Summit, Eldorado Co., CA; Hughes Canyon, Salt Lake Co., Utah; and especially Shaver Lake, Fresno Co., CA. However, specimens from Alaska, British Columbia, and Washington are all strongly

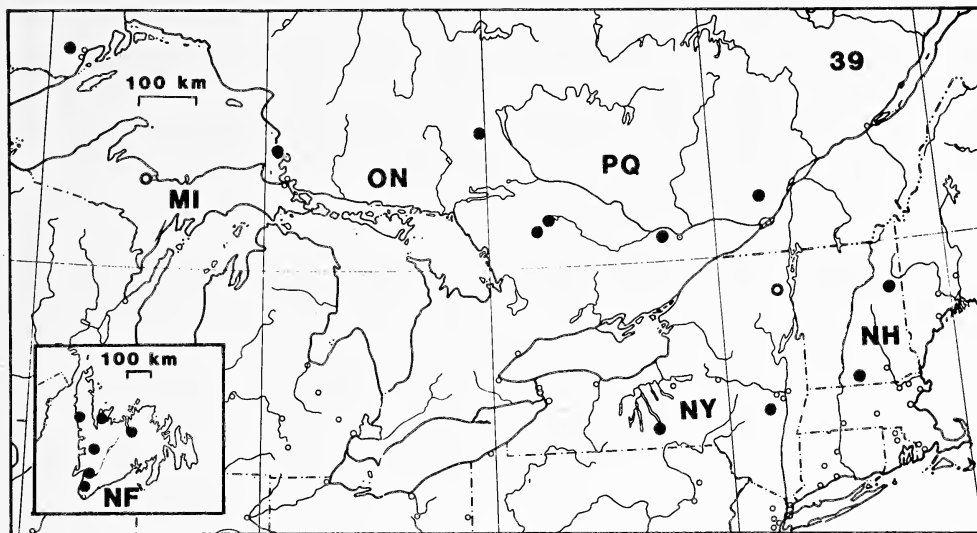


Fig. 39.—Distribution of *Cybaeota calcarata* in eastern North America (inset—Newfoundland). Hollow circles—literature records (Chickering 1935; Crosby and Bishop 1928).

patterned with the spinnerets encircled with pigment and a typical “cheshire cat face” on the epigastric area. As well, most concolorous or faintly patterned individuals come from the possibly disjunct population in Utah (originally described as *C. wasatchensis*). Spiders from this population are generally larger than the coastal spiders (average female CL 1.05 mm versus 0.91 mm).

The lack of specimens from S Idaho and N Nevada makes a definite conclusion with respect to the clinal nature of the variability of size and abdominal pattern (as well as the disjunct nature of the Utah population) difficult. Still, I feel the observed pattern variability in other species of *Cybaeota* and the clinal variation in pattern and size observed in *C. nana* over the range it shares with *C. shastae* coupled with the identical morphology of the genitalia of specimens previously placed in *C. wasatchensis*, *C. vancouverana*, and *C. shastae* justifies the identity of all such species with *C. shastae*.

Material examined.—*Types*: Holotype of *C. shastae*, CALIFORNIA; Siskiyou Co., Weed, 8 IX 1935 (W. Ivie and R. V. Chamberlin), 1 male, 2 females (allotype and paratype) (AMNH). Holotype of *C. wasatchensis*, UTAH; Salt Lake Co., Hughes Canyon, Wasatch Mtns., 20 V 1934 (Ivie and Rasmussen), 1 male (plus 1 female allotype) (AMNH). Holotype of *C. vancouverana*, BRITISH COLUMBIA; Sidney, 16 IX 1935 (R. V. Chamberlin and W. Ivie), 1 female (AMNH).

CANADA: BC; Vancouver Is., Bowser, 25 VI 1955, 1 female (CNC), Cowichan Lk. Exp. Stat., 25 VII 1975 (REL), 2 females, 3 imm. (CNC), Kyuquot, 50°00'N/127°25'W, 2 V 1952 (S. L. Neave), 1 female (CNC), 22 IV 1959, 1 female (AMNH), 19 V 1959, 2 females, 1 imm. male (AMNH), Shawnigan Lk., 9.1 mi. W E+N RR tracks, Pt. Renfrew Rd., 14 VIII 1985 (R. G. Bennett), 4 females, 17 imm. (RGB), Sidney, 16 IX 1935 (R. V. Chamberlin, W. Ivie), 1 female (AMNH), Victoria, XI 1975 (D. State), 1 female (CNC), Victoria, Francis Regional Pk., Munn's Rd., 2-12 VIII 1985 (R. G. Bennett), 12 males, 23 females, 13 imm. (RGB), Victoria, Goldstream Pk. (A. P. Mackie), 16 I 1975, 1 female, 14 IV 1975, 2 females, 24 IV 1975, 2 females, 23 VII 1975, 1 female, 7 VIII 1975, 1 male, 1 imm. (all CNC), 23 IX 1975 (B. Ainscough), 1 female (CNC). USA: AK; Admiralty Is., Middle Hbr., 20 VI 1932 (A. Hasselborg), 2 males (AMNH), Admiralty Is., VI 1933 (Sheppard), 1 male, 1 female (AMNH), Juneau, 28-29 IV 1945 (J. C. Chamberlin), 1 imm. (AMNH). CA; “Redwoods”, 1 male (AMNH); Eldorado, Lk. Tahoe, Echo Summit, 7382', 2 IX 1961 (W. J. Gertsch, W. Ivie), 1 male, 1 female (AMNH), Meyers, 7000', 25 VI 1953 (V. Roth), 1 male (CAS); Fresno, Shaver Lk., 12 IX 1959 (W. J. Gertsch, V. Roth), 7 males, 6 females, 1 imm. (AMNH); Humboldt, Trinidad, 16 VII 1968 (W. Ivie), 2 females (AMNH); Shasta, Lassen Volc. Nat. Pk. 7000', 19 IX 1961 (W. J. Gertsch, W. Ivie), 1

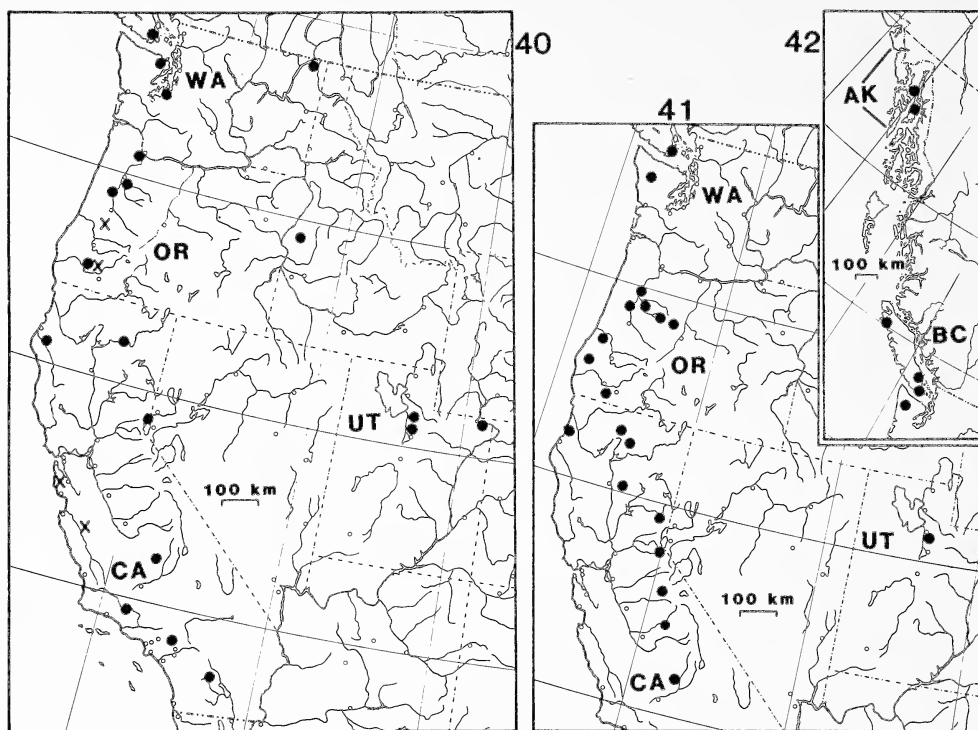


Fig. 40.—Distribution of *Cybaeota munda* (crosses) and *C. nana* (circles) in western North America. Figs. 41, 42.—Distribution of *C. shastae*: 41, western USA; 42, BC and southern AK.

male (AMNH), Lassen Pk., 2 mi. NE Manzanita Lk., 6150', 8 VIII 1968 (R. E. and A. V. Leech), 1 male (REL); *Sierra*, 2 mi. N Calpine, 6 IX 1959 (W. J. Gertsch, V. Roth), 2 females (AMNH); *Siskiyou*, Bartle, 18 IX 1961 (W. Ivie, W. J. Gertsch), 1 female (AMNH), Mt. Shasta, Panther Meadow Rd., 41°23'N/122°12'W, 17 IX 1961 (W. J. Gertsch, W. Ivie), 1 female (AMNH), Weed, 8 IX 1935 (R. V. Chamberlin, W. Ivie), 1 female (AMNH); *Tulare*, 6 mi. W Johnsondale, Double Bunk Meadows, 15 IX 1959 (V. Roth, W. J. Gertsch), 1 female (AMNH); *Tuolumne*, Yosemite Nat. Pk., Aspen Valley, 11 VIII 1931 (W. Ivie), 2 males, 2 females (AMNH). OR: Boyer (45°N/123°W ?), 10 VIII 1933 (J. C. Dirks), 1 female AMNH, 15 mi. W Burnt Woods, 30 XII 1945 (R. Post), 1 female (AMNH); *Benton*, Corvallis, 12 V 1953 (V. Roth), 1 female (CAS), 9 mi. W Philomath, 29 VII 1953 (W. J. and J. W. Gertsch), 1 female (AMNH); *Coos*, Bridge, Myrtlewood Camp, 27 VII-4 VIII 1955 (V. Roth), 1 female (CAS); *Douglas*, Loon Lk., 1 VII 1959 (L. M. Smith), 1 female (AMNH); *Jackson*, 20 mi. NE Ashland, 1 IX 1959 (W. J. Gertsch, V. Roth), 1 female (AMNH); *Linn*, Berlin, 23 IV 1954 (Roth, Davis), 1 female (CAS), Santiam Pass, Suttle Lk., 27 V 1947 (V. Roth, F. Beer), 1 female (CAS), Santiam Pass, Tombstone Prairie, 13 VIII 1949 (V. Roth), 1 female (CAS); *Josephine*, 1 male, 1 female, 2 imm. (AMNH); *Marion*, Salem, 1 V 1954 (V. Roth), 1 female (CAS). UT: *Salt Lake*, 40°N/111°W, 3 males, 5 females (AMNH), Hughes Can., nr. Holladay, 20 V 1934 (W. Ivie), 1 male, 2 females (AMNH), Mill Ck. Can., 8 IV 1932 (W. Ivie), 1 female (AMNH), 1-2 mi. up Mill Ck. Can., 21 VIII 1941 (J. C. Chamberlin), 1 male, 1 female (AMNH). WA: *Jefferson*, Olympic Nat. Pk. Hoh R., 3 VIII 1954 (C. J. Goodnight), 4 females (AMNH).

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RESEARCH NOTES

**DRAGONFLY PREDATION UPON
PHIDIPPUS AUDAX (ARANEAE, SALTICIDAE)**

Dragonfly adults are aerial predators capable of capturing prey in the air or from exposed surfaces. Spiders that hunt on exposed surfaces or that balloon from prominences should be potential prey for dragonflies. A review of the predators of spiders (Bristowe 1941) indicates that dragonflies are very seldom recorded capturing spiders, with only three observations listed from British Guiana, Costa Rica, and India. Reviews of the known prey of adult dragonflies (Corbet 1962, 1980), reveal only one record of predation on spiders, that of a *Megalagrion* sp. removing a salticid from a fern leaf in Hawaii (Williams 1936). Members of the Salticidae may be more exposed to dragonfly predation than other spiders that hunt in the canopy of the herbaceous layer, due to their general lack of crypticity as compared to the Thomisidae and to their relatively active mode of hunting. The Salticidae literature is equally depauperate in records of dragonfly predation. In a review of the ecology of *Phidippus* spp. in eastern North America, Edwards (1980) reports his own observation of an adult *Erythemis simplicicollis* (Say) (Libellulidae) preying upon an immature *Phidippus pulcherrimus* Keyserling.

Apparently there is some risk associated with a dragonfly attempting to capture a jumping spider. Fitch (1963) observed an adult *Phidippus audax* (Hentz) jumping several inches into the air in unsuccessful attempts to capture adult dragonflies overhead and on other occasions observed *P. audax* carrying dragonflies. Edwards (1980) presents two additional records of *P. audax* and *P. otiosus* (Hentz) capturing adult Libellulidae. The purpose of this report is to document the behavior of a salticid in the presence of patrolling adult dragonflies and to record an instance of successful spider capture by an adult dragonfly.

During the period 15-29 October 1986, visual censuses of foliage arthropods were conducted daily in a 0.1 hectare plot in Washington County, Mississippi (Young in Prep.). This plot contained a variety of weed species and three rows (length = 25 m) of nectaried cotton that had not been picked and was reflowering. Each day several individuals of *Epiaeschna heros* Fab. (Aeschnidae) were observed patrolling lengthwise the rows of cotton, flying 0.3-0.7 m directly above each row. Individuals of *P. audax* on many occasions were also observed near the very top of these cotton plants, usually in a position that gave them some protection from the rear and that allowed them to view an adjacent plant and some of the leaf surfaces below them. Individuals of *P. audax* seemed to be quite capable of detecting an approaching dragonfly at a distance of approximately 3 m, perhaps aided by a moving silhouette of the dragonfly against a bright sky background. At that distance, the spider oriented its body so as to be directly

facing the oncoming dragonfly and assumed a position indicating a readiness to jump. Dragonflies were not observed to alter their flight path when approaching and passing over *P. audax* individuals, and the spiders were not observed to jump. On several occasions when a dragonfly seemed to be moving rather slowly along the row, *P. audax* individuals continually reoriented themselves so as to be facing the dragonfly at all times.

On those warm and sunny days in which the wind exceeded approx. 3 mph, *P. audax* individuals frequently occurred at the top of plants in a ballooning posture. During one census of a single cotton row (25 m), 17 of 21 *P. audax* were at the top of plants spinning silk lines for either ballooning or for traverse lines to adjacent plants. The typical posture involved the downward inclination of the cephalothorax 40-80° below the horizontal, with the abdomen pointed upward in a near vertical position. When *P. audax* assumes this position an aerial predator, approaching from the spider's rear or ventral side, might be able to avoid detection and affect capture.

At 1000 hours, 19 October 1986, an adult female *P. audax* was in a ballooning posture on top of a seedhead of Johnson-Grass (*Sorghum halepense*) at a height of 2 m. The wind was from the west and the spider was positioned such that the ventral side of its abdomen was facing west. An adult of *E. heros* was observed approaching the spider from the west at a height of 2 m and was first seen by us when it was 5 m from the spider. The dragonfly flew in a straight line to the spider, grabbed it in its legs, and continued flying in the same direction and at the same height until it was out of sight at a distance of approx. 75 m. The body length of the *E. heros* was probably in the range of 82-91 mm with a wing span > 110 mm (Needham and Westfall 1955). The body length of the *P. audax* female was probably about 13 mm, based on an average value from 15 adult females captured and measured during the census period.

Our observations on the response of *P. audax* to foraging dragonflies and the successful capture of *P. audax* by *E. heros* lead us to believe that dragonflies in late summer and fall may be significant predators on spiders attempting to disperse.

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NOTES ON AGGREGATIONS OF *LEIOBUNUM* (OPILIONES) IN THE SOUTHERN U.S.A.

Aggregations of phalangids of the genus *Leiobunum* C. L. Koch are known from caves and mines (Holmberg et al. 1984; Mitchell and Reddell 1971), lake shores (Bishop 1950), rock overhangs (Newman 1917), buildings (McAlister 1962), and vegetation (Edgar 1971; Wagner 1954). Such formations may represent: (1) diurnal retreat aggregations (McAlister 1962; Wagner 1954), covering sometimes 25 ft² in area (Newman 1917); (2) overwintering aggregations, for which densities of nearly three individuals/cm² are reported (Holmberg et al. 1984); (3) smaller and more loosely organized groups apparently associated with mating (Edgar 1971).

Phalangids in retreat aggregations are quiescent except for movements associated with changes in microclimate (Holmberg et al. 1984; McAlister 1962). When disturbed, however, individuals move their bodies to-and-fro. This "bobbing" can quickly spread through an entire cluster of thousands, presumably by mechanical stimuli transmitted via legs (Newman 1917). This behavior is often accompanied by the release of volatile compounds (Holmberg et al. 1984; Ekpa et al. 1985), which may act to deter predators (Blum and Edgar 1971), although functions associated with intraspecific communication have been suggested for phalangid secretions (Bishop 1950).

While observing phalangids in the southcentral U.S.A., I noted both homospecific and heterospecific aggregations of *Leiobunum* species. Aggregations are reported for the first time for *Leiobunum flavum* Banks and *Leiobunum speciosum* Banks. Immatures of another species, *Leiobunum townsendi* Weed, whose prodigious aggregating habit is described elsewhere (McAlister 1962; Mitchell and Reddell 1971), are confirmed to form aggregations. Identifications of species are based on Bishop (1949) and Davis (1934) with reference to the nomenclatural changes proposed by Cokendolpher (1984).

Homospecific aggregations.—I removed an aggregation of *L. townsendi* from the duck blind at The University of Texas Brackenridge Field Laboratory, Austin, Travis Co., Texas at 1600 hours on 20 September 1985. This diurnal retreat aggregation was a single layer of 167 males and 157 females covering an area of 300 cm² on the underside surface of the wooden platform. This density (1.1 individuals/cm²) has also been calculated by Holmberg et al. (1984) for the less tightly formed clusters of *Leiobunum paessleri* overwintering in caves and mines of British Columbia. He also reports equal proportions of the sexes.

I found late instars of *L. townsendi* in aggregation on the stone block restroom at the trailhead to the falls at Pedernales Falls State Park, Blanco Co., Texas. At 1200 hours on 18 April 1987, I counted 331 individuals of this species on the building, 282 within 14 aggregations (of from 6 to 70 individuals) and 49 outliers. All were in shade on the east, west, or north sides. The majority of them (64.3%) were in the window recesses, which are poorly exposed, the rest on the upper half of the walls. Two clusters of 19 and 21 were sampled and contained immatures, the ages of which were estimated morphometrically (Edgar 1971, table 3). A sample of seven individuals taken from one of these included one fourth, three sixth, and three seventh (penultimate) instars. I located two other clusters of *L. townsendi* along the trail to the falls. One of these contained 31 phalangids

loosely aggregated on the brick wall at the falls overlook. The second was more dense (like that on the duck blind), containing 150 individuals clinging to the underside of a rock ledge about 50 m upriver from the first. Both groups were composed largely of late instars. I found another cluster of this species at the boulder field above the falls. Within a shallow crevice in a large rock, 15 phalangids had formed a continuous single file. From this I sampled nine penultimates and one adult male. Another cluster on the smooth, lower face of the rock, just above the river, consisted of about 50 phalangids, at least nine of which were sixth or seventh instars.

I found two small clusters of *Leiobunum aldrichi* Weed in the late morning of 19 July 1986 at the summit of Mount Magazine, Logan Co., Arkansas. Both males and females were loosely grouped, making contact only with the tarsi. One cluster of about 20 had formed on the underside of a rock ledge just above the outflow of Brown Springs. Another group of six was seen about a kilometer from the first in a hollowed-out area on the rock face near the head of the Cove Lake Trail.

Diurnal retreat aggregations have not yet been reported for *L. aldrichi* and there is both field and laboratory evidence that northern populations show diurnal activity (Bishop 1950; Edgar and Yuan 1968; Fowler and Goodnight 1974). Bishop (1950) observed clusters of this species forming late in the day at the edge of a lake in a New York beech-hemlock forest. These were apparently associated with relief from unfavorable microclimate and lasted until the next morning. Edgar (1971) observed gatherings of this species (on tree trunks in a Michigan woodland) that were suggestive of prenuptial behavior. These consisted of groups of from 3 to 58 males and females which remained together for a few days until males began attempting to copulate. I kept records of activity for this species in an oak-pine forest in Tennessee from May through August, 1981. During 46 sample days, I observed five copulation attempts (between 1935 hours and 0150 hours) but none were associated with clusters. During the daytime, when *L. aldrichi* is inactive on trunks, I never observed more than three individuals spaced closely enough to contact legs. It is, therefore, impossible to identify this species with a single, regularly occurring type of aggregation.

An aggregation of about 100 phalangids was found on the wall of a wooden shelter on the morning of 21 July 1985 near Lake Seminole, Jackson Co., Florida (L. Hribar, pers. comm.). I identified a female specimen from the aggregation as *L. speciosum*. (Voucher specimen is deposited at the Texas Memorial Museum). A photograph showed that this was probably a single species group but sexes could not be distinguished.

Heterospecific aggregations.—At Caddo Lake State Park, Harrison Co., Texas, I found a highly clumped distribution of three species of *Leiobunum* under the eaves of a campground shelter. On 25 June 1986 at 2100 hours, 12 well defined aggregations were present, separated from one another by rafters. Single individuals were seen crawling along the edges of the roof. By visually comparing the area covered by each cluster to that for one I counted, I was able to estimate the numbers of phalangids within clusters. Starting at the NE corner and moving counterclockwise around the shelter, I estimated clusters of 25, 30, 250, 100, 175, 225, 300, 150, 20, 50, and 25 individuals. (The one at the SW corner was too loosely formed to estimate.) The majority of phalangids were on the north and west sides of the shelter. Density within groups was less than one phalangid/cm².

A sample from the cluster of 50 showed 18 males and four females of *L. flavum*. (Voucher specimens are deposited at the Texas Memorial Museum). This species accounted for at least 90% of all phalangids in any given cluster. The rest were *Leiobunum vittatum* (seen in four clusters) and *L. townsendi* (seen in two). The cluster at the SW corner contained all three species. Aggregations of *L. flavum* have not previously been reported. Small bisexual clusters of *L. vittatum* were seen in summer by Edgar (1971).

In checking the aggregations for activity at 2200 hours, I saw three phalangids at the perimeter of the loose cluster feeding together on an insect. I did not see copulating pairs in or near any of the groups. When I disturbed one large cluster by moving my pencil through it, a chain of phalangids dropped and hung by the legs from those above. Within seconds, the suspended ones became disentangled, fell to the ground, and began to crawl toward the shelter and up the wall.

At 2300 I noted no changes in the aggregations, but at 0900 hours there was a marked difference in their dispersion. The loosely formed aggregation had disbanded, while another group had decreased in numbers from 100 to 50 individuals. Two clusters had increased in size, one from 150 to 250, the second from 20 to 125. All clusters were more dense ($> \text{one individual/cm}^2$) than at night and showed no activity. No solitary phalangids could be found on the shelter. I made a final check of the aggregations at 1230 hours but saw no change.

I observed aggregations consisting of both males and females of *L. flavum* and *L. vittatum* at two locations in western Arkansas, each occurring beneath the eaves of campground buildings. These sightings were made at 1000 hours on 20 July 1986 at Cove Lake, Logan Co. and at 1100 hours on the following day at DeQueen Lake, Sevier Co.

Conclusion.—Aggregations of *Leiobunum* are more common than has been reported. I here add *L. flavum* (in Arkansas and Texas) and *L. speciosum* (in Florida) to the list of *Leiobunum* species forming diurnal retreat aggregations. Clusters of more than one phalangid species are also reported for the first time.

Aggregations were observed in spring (when immatures may be present in them) and in summer, primarily on structures providing considerable shade. All were diurnal except for a group of nocturnal clusters at one location, which were more active and loosely organized.

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DEVELOPMENT OF *PHOLCUS PHALANGIOIDES* (FUESSLIN) (ARANEAE, PHOLCIDAE) UNDER LONG AND SHORT PHOTOPERIODS

Pholcus phalangioides (Fuesslin) commonly inhabits buildings and therefore leads a normal life even under the strong influence of human activities, especially lighting and air conditioning. In the present study the effect of photoperiod on the development of this spider was investigated to clarify the reason why it is able to settle easily in buildings.

Five egg-sac-carrying females were collected from the animal rearing room of Tokyo Metropolitan University, Tokyo, in late May of 1984. The first-instar nymphs obtained from these females were kept individually in plastic vessels 5.7 cm in diameter \times 11.0 cm in height for the first to third instar period and in vessels measuring 11.4 cm \times 25.2 cm thereafter. A strip of thick paper was placed slantways in each vessel as a substrate. In order to investigate the effect on development of photoperiod and complete darkness, four groups each consisting of six individuals were prepared. Two groups were reared at 25°C under a long (16L-8D) or short (10L-14D) photoperiod, and two at 23.5°C under either complete darkness or 14L-10D. The light source was a 6W fluorescent tube, producing a light intensity of 250-300 lux. Relative humidity was not controlled, but fluctuated between 50 and 80%. Since first-instar nymphs molt without feeding, food supply was initiated at the second instar stage. The 2nd and 3rd-instar nymphs were alternately provided fruit flies, *Drosophila melanogaster*, and

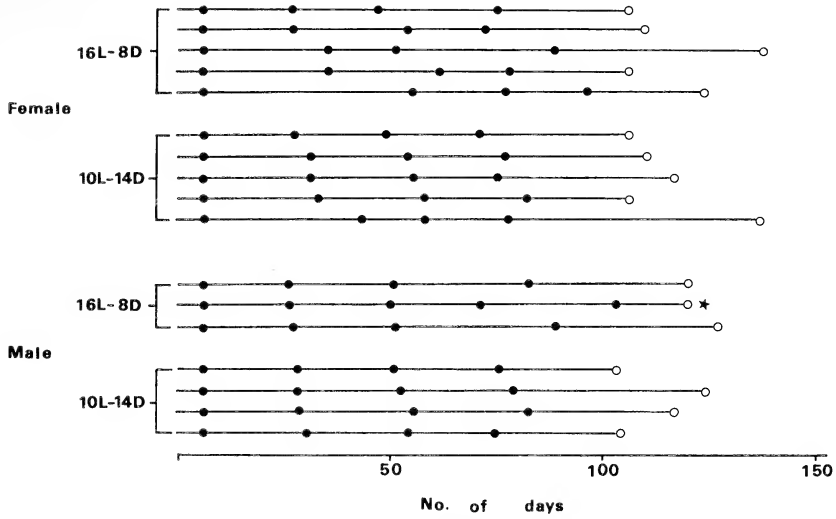


Fig. 1.—Developmental processes of *Pholcus phalangioides* nymphs reared at 25°C under long (16L-8D) or short (10L-14D) photoperiod. Solid circles indicate moltings, and clear ones final moltings. The horizontal line with a star indicates the male that molted six times.

planthoppers, mainly *Saccharosyden procerus*. The number of prey provided was increased from 1-2 to 3-5 as development proceeded. The nymphs from 4th-instar to the final molt were provided with a fly, *Phaenicia sericata*, each time. The feeding interval was every 3 or 4 days. Experimental animals reared under complete darkness were exposed to light for a few minutes at each feeding and vessel change. Individuals dying during the rearings were omitted from the graphs subsequently obtained.

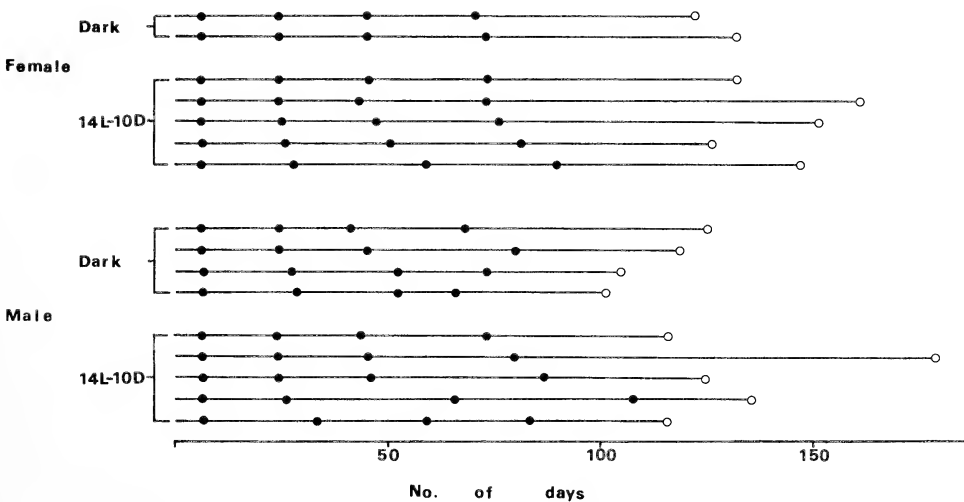


Fig. 2.—Developmental processes of *Pholcus phalangioides* nymphs reared at 23.5°C under complete darkness as compared with that of spiders reared under 14L-10D. Symbols are the same as for Figure 1.

Table 1.—Growth as indicated by carapace width in *Pholcus phalangioides* reared at 23.5°C under 14L-10D. Figures in parentheses indicate those for adults collected from natural habitats.

| | INSTAR | | | | | ADULT | |
|---------------|-----------|-----------|-----------|-----------|-----------|--------------------------|--------------------------|
| | 1 | 2 | 3 | 4 | 5 | Female | Male |
| No. of indiv. | 15 | 13 | 8 | 11 | 5 | 15(12) | 14(12) |
| Mean (mm) | 0.63 | 0.67 | 0.98 | 1.31 | 1.75 | 1.85(2.10) | 1.74(2.09) |
| Range (mm) | 0.59-0.66 | 0.63-0.72 | 0.91-1.03 | 1.25-1.38 | 1.66-1.88 | 1.63-2.19 (2.00-2.38) | 1.63-1.81 (1.94-2.30) |

First-instar nymphs molted without feeding by the 5-6th day after emergence and showed tolerance to fasting. The mean and range of longevity for 30 fasting nymphs kept individually at 23.5°C under 14L-10D were 31.8 and 22-40 days.

Figure 1 shows the result of rearings at 25°C under a long or short photoperiod. All the individuals reared under both photoperiods completed their development within a period ranging from 100 to 140 days. For females, the mean developmental period was calculated to be 116.8 days under the long photoperiod and 115.2 days under the short one. The same calculation for males gave means of 122.3 and 112.0 days, respectively. This difference of 10.3 days between the 2 photoperiods for males was insignificant (*t*-test). The number of molts was five for both sexes, except for one male which molted six times. In other words, development of the spiders was practically unaffected by photoperiod. According to Schaefer (1977, *Z. ang. Entomol.*, 83:113-134), the development of many spider species is closely connected with changes in temperature and photoperiod, and reactions to photoperiod differ among species. Hamamura (1982, *Japanese J. Appl. Entomol. Zool.*, 26:131-137) also ascertained that in *Philodromus subaureolus* Boesenberg et Strand, the effect of photoperiod on development was reversed before and after overwintering.

Figure 2 shows the result of rearing under complete darkness as compared with that under 14L-10D, revealing that *P. phalangioides* developed normally even under complete darkness. In addition, the developmental period for males showed a tendency to become shorter under complete darkness than under 14L-10D. The means were calculated to be 112.5 days under complete darkness and 134.3 days under 14L-10D, but this difference of 21.8 days was statistically insignificant. According to Miyashita (1987, *J. Arachnol.* 15:51-58), *Achaearanea tepidariorum* (C. L. Koch) developed more rapidly in darkness than under light, accompanied by a reduction in the number of molts.

Table 1 shows the growth of *P. phalangioides* as indicated by carapace width. Measurements were performed on the individuals reared at 23.5°C under 14L-10D. After each molt, several individuals were placed into 75% alcohol for preservation and measurement. As shown by the figures in the last column, the mean carapace width of adults was somewhat larger in individuals collected from natural habitats than in those reared artificially. The difference between them was 0.34 mm in females and 0.37 mm in males, but was not significant (*t*-test: $P > 0.2$ in the former and $P > 0.05$ in the latter). A similar observation was reported for *Clubiona phragmitis* C. L. Koch by Schaefer (op. cit.) and also for *A. tepidariorum* by Miyashita (op. cit.). However, the reason for this was unknown, except for the possible effect of a simple diet.

It can thus be concluded from the results described above that the reason why this species is able to settle easily in buildings is its apparent insensitivity to light during development.

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EGG PRODUCTION IN *PHOLCUS PHALANGIOIDES* (FUESSLIN) (ARANEAE, PHOLCIDAE) UNDER A CONSTANT TEMPERATURE AND PHOTOPERIOD

Egg production in *Pholcus phalangioides* (Fuesslin) was examined. Ten final-instar female nymphs were collected from the animal rearing room of Tokyo Metropolitan University, Tokyo, in early June of 1984, and kept individually in plastic vessels 11.4 cm in diameter \times 25.2 cm in height. In each vessel, a strip of thick paper was placed slantways as a substrate. After the spiders had been reared to the adult stage in the laboratory, they were mated with males obtained in the same way, and reared individually in the above-mentioned vessels until the time of death, being provided one fly, *Phaenicia sericata*, at intervals of 3-4 days. Five of these individuals were subjected to a second or third mating at different periods of their life, as shown in Fig. 1. An additional seven females were collected just after they had mated in natural habitats, and three of them were also subjected to a second mating in the laboratory. The time of collection was within five days after their final molt.

Egg-sac production and the emergence of first-instar nymphs were recorded during the whole period of rearing, and the number of eggs per sac was determined as the number of first-instar nymphs which emerged from an egg-sac plus dead (unfertilized) eggs remaining in the sac. Dead nymphs were counted as fertilized eggs.

The rearing room was maintained at 23.5°C under 14L-10D. Light was provided by 40 W fluorescent tubes, which gave a light intensity of 600-800 lux. Relative humidity was not controlled, but fluctuated within a range of between 50 and 80%.

Figure 1 shows egg-sac production by 17 females. The females numbered 1-10 in the graph produced their first egg-sac 6-13 days after mating, the mean pre-oviposition period being 9.6 days. The period from oviposition to the emergence of first-instar nymphs varied from 17 to 24 days, with a mean and standard deviation (calculated from 44 egg-sacs indicated by solid circles in the graph) of 19.9 ± 1.34 days. A large number of females continued oviposition for 400 days or more. In natural habitats, however, egg-sac-carrying females were generally found for only 100-120 days, from middle or late May to late August or early September.

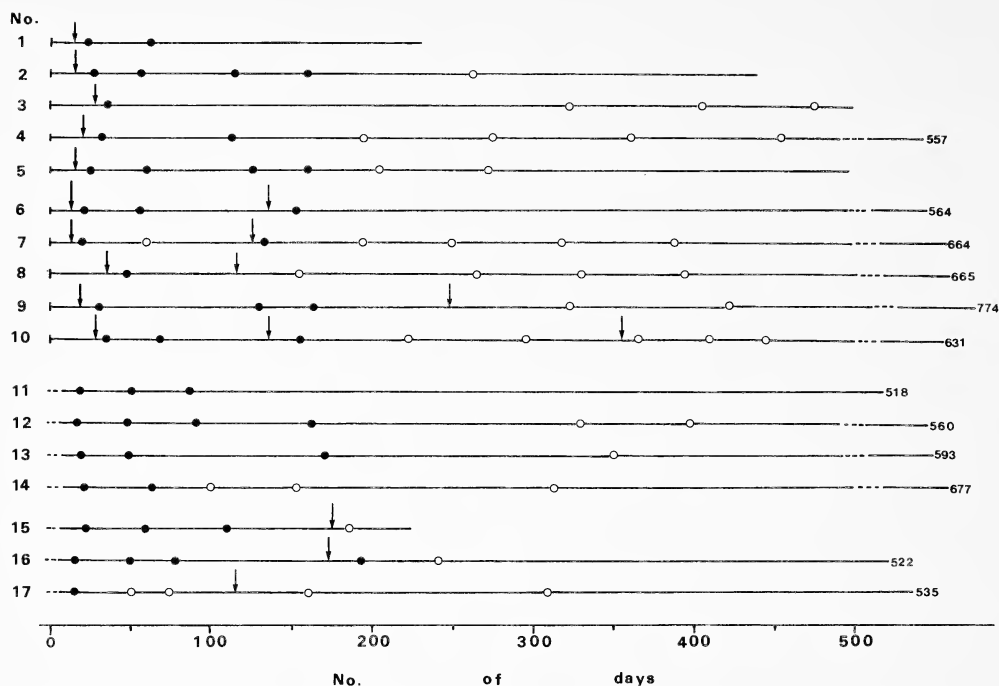


Fig. 1.—Occurrences of egg-sac production in 17 female *Pholcus phalangioides*, of which 10 (nos. 1-10) mated in the laboratory and 7 (nos. 11-17) did so in natural habitats. Solid circles indicate egg-sacs from which spiderlings emerged, and clear ones those that contained unfertilized eggs only. Arrows show matings in the laboratory. The figure following each line represents the life span of each individual in days.

The number of egg-sacs produced per female varied from 2 to 8, with a mean of 4.9 sacs. Egg-sac production intervals were irregular, and showed a tendency to become longer as time passed. The total number of eggs produced per female varied from 48 to 224, with a mean of 124.5, and the mean fertilization rate was 51.5%. Therefore, the mean number of fertilized eggs produced per female was 64.1.

According to the data for females numbered 6-10 and 15-17 in the graph, additional mating(s) showed almost no effect upon fertilization rate. This was considered not to have resulted from incomplete second or third matings, because the durations of the latter matings were similar to those of the first ones: mean and range of mating duration were 86.7 and 34-138 minutes in the former ($n=9$) and 65.9 and 22-98 minutes in the latter ($n=10$). The actual reason for the presence of unfertilized eggs remains unknown.

As shown in Table 1, the majority of the first, second and third egg-sacs contained a mixture of fertilized and unfertilized eggs, although the percentage of egg-sacs containing only fertilized eggs was somewhat higher in the first egg-sac. The fifth and subsequent egg-sacs contained unfertilized eggs only. The total number of eggs per sac, including fertilized and unfertilized ones, gradually decreased with time. Such a tendency has been described in many species of spiders, but few authors have reported the exact state of fertility of eggs in each sac. Miyashita (1987, J. Arachnol. 15:51-58) noted that a similar tendency to that shown in Table 1 was also observed in *Achaeearanea tepidariorum* (C. L. Koch),

Table 1.—Levels of egg production in relation to egg-sac sequence in *Pholcus phalangioides*. Figures in parentheses represent unfertilized eggs.

| INDIVIDUAL NUMBER | EGG-SAC SEQUENCE | | | | | | | | TOTAL EGGS | |
|----------------------|------------------|--------|-------|--------|------|------|------|-----|------------|--------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | Fertilized | Unfertilized |
| 1 | 27 | 30 | | | | | | | 57 | 0 |
| 2 | 29 | 22 | 32 | 12(10) | (12) | | | | 95 | 22 |
| 3 | 28(2) | (16) | (10) | (6) | | | | | 28 | 34 |
| 4 | 20 | 38(2) | (36) | (29) | (17) | (5) | | | 58 | 89 |
| 5 | 26(3) | 37 | 47(2) | 22(4) | (25) | (33) | | | 132 | 67 |
| 6 | 42(1) | 28(1) | 26(2) | | | | | | 96 | 4 |
| 7 | 35(2) | (35) | 33(4) | (27) | (47) | (32) | (9) | | 68 | 156 |
| 8 | 10(2) | (10) | (14) | (11) | (16) | | | | 10 | 53 |
| 9 | 32 | 15(15) | 5(29) | (18) | (28) | | | | 52 | 90 |
| 10 | 31 | 26 | 27(6) | (27) | (23) | (28) | (14) | (6) | 84 | 104 |
| 11 | 7(11) | 7(3) | 9(11) | | | | | | 23 | 25 |
| 12 | 34(3) | 19(13) | 21(8) | 19(9) | (31) | (14) | | | 93 | 78 |
| 13 | 27 | 16 | 19(9) | (29) | | | | | 62 | 38 |
| 14 | 7(11) | 13(3) | (18) | (30) | (21) | | | | 20 | 83 |
| 15 | 20(9) | 18(1) | 5(7) | (15) | | | | | 43 | 32 |
| 16 | 26(13) | 25(5) | 52 | 34(4) | (35) | | | | 137 | 57 |
| 17 | 31 | (47) | (27) | (13) | (7) | | | | 31 | 94 |
| \bar{X} no./sac | 28.8 | 26.2 | 28.7 | 22.8 | 23.8 | 22.4 | 11.5 | 6.0 | 64.1 | 60.4 |
| % fertility | 88.3 | 66.1 | 60.1 | 27.3 | 0.0 | 0.0 | 0.0 | 0.0 | | |

although the eggs in each sac were either all fertile or all infertile, and the mean fertilization rate was rather high as compared with that in *P. phalangioides*. However, Downes (1985, Australian J. Ecol. 10:261-264) reported that the number and fertility of eggs in *Latrodectus hasselti* Thorell fluctuated independently of egg-sac sequence.

In the present study, the life span of adult spiders varied from 223 to 774 days, with a mean of 538.4 days. These figures are slightly lower than those for American black widow spiders, *Latrodectus mactans* (Fabricius), *L. variolus* Walckenaer and *L. hesperus* Chamberlin and Ivie, as reported by Kaston (1970, Trans. San Diego Soc. Natur. Hist. 16 (no. 3), 82 pp). In males reared under the same conditions as these females, adult life span varied from 132 to 277 days, with a mean of 179.8 days ($n=11$ individuals that experienced mating(s)).

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**INTERACTIONS BETWEEN THE CRAB SPIDER
MISUMENA VATIA (CLERCK) (ARANEAE)
AND ITS ICHNEUMONID EGG PREDATOR
TRYCHOSIS CYPERIA TOWNES (HYMENOPTERA)**

Spider egg masses are subject to a wide variety of dangers, including insects whose larvae require them as a food source. Information on these spider-insect relationships often consists largely of documenting predator and prey species (Askew 1971), and in many instances even predator or parasitoid records are missing (Krombein et al. 1979; Austin 1985).

In my study area along the coast of Maine, U.S.A., the ichneumonid wasp *Trychosis cyperia* Townes (Hymenoptera: Ichneumonidae) is an egg predator on the crab spider *Misumena vatia* (Clerck) (Araneae: Thomisidae). I define an egg predator as an individual that attacks the eggs of a mass collectively and feeds externally on it, rather than developing within a single egg oviposited there by its parent (Austin 1985). A single larva of *T. cyperia* will totally consume all but the largest of *Misumena* egg masses, before pupating within the spider's nest (Morse and Fritz 1987).

Trychosis is a potentially important egg predator on *Misumena*, since one successful attack usually totally destroys the spider's entire reproductive effort (Morse and Fritz 1987). Further, *Trychosis* may successfully attack between 7 and 60% of the *Misumena* nests in a local population (Morse and Fritz 1987; Morse, unpublished data).

As a result of *Trychosis*' high predation level, *Misumena* should experience strong selection to minimize wasp attacks. Indeed, female *Misumena* guard their egg masses over much or all of the period between egg-laying and emergence of the young from the nest about a month later (Morse 1985). Predation by these wasps is not random: they successfully attack small egg masses, which are guarded by small spiders, significantly more frequently than large ones. This pattern is a consequence of differences in guarding behavior by different-sized spiders. Nests from which the parents are removed do not differ in success as a consequence of egg mass size (Morse, unpublished data).

This result strongly suggests that the differential predation is a consequence of direct interactions between *Misumena* and *Trychosis*, in which large spiders fare better than small. However, although I monitored the nesting success of over 200 spiders at three different sites between 1982 and 1985, I did not observe *Trychosis* adults in the field, even though predation by it was sometimes high.

During the summer of 1986, I finally observed *Trychosis* at *Misumena* nests, and the response of guarding *Misumena* to them. I have been unsuccessful in finding reports of similar interactions in the literature, and therefore describe them in detail, both to document their characteristics and to draw them to the attention of others who might be in a position to observe similar behavior.

In the first observation, a brief encounter, a *Trychosis* landed on the upper surface of a *Misumena* nest, located in a turned-under leaf, 40 cm up a milkweed plant (see Morse 1985 for a description of *Misumena* nests). After a few seconds, it moved out of view over the side of the nest to the under surface, flicking its wings and abdomen rapidly. It encountered the guarding female crab spider and

instantly flew from the nest and out of sight. The spider's front legs were raised at the instant after the wasp left, a pattern I have otherwise only observed when a spider is ready to strike at prey (Morse 1979). The spider lowered her legs within 10 sec. This ichneumon did not probe the nest with its ovipositor while it was within sight; indeed the brood it visited was 19 days old; therefore, the spiderlings inside probably were nearly ready to molt into their second instar, and it seems unlikely that an egg predator would be able to exploit this nest successfully. This nest was not parasitized, and young eventually emerged from it. This female weighed 74 mg after egg-laying, near the average mass for post-reproductive females of this population in 1986 ($\bar{X} \pm \text{SD} = 76.7 \pm 20.4$ mg., $N = 171$).

The second encounter was much more protracted, and involved an eight-day-old nest guarded by an extremely large female spider (114 mg). I initially observed the ichneumon on a leaf 45 cm above the ground, near the top of a milkweed plant, three cm from an adjacent leaf with a *Misumena* test. Initially the wasp was largely stationary, although its antennae remained in constant motion. At that instant the spider occupied the underside of her nest out of the direct line of vision from the wasp. After 30 sec the ichneumon became active and walked about in a tight circle for about 30 sec before taking its previous position. Two minutes later it moved to the underside of its leaf. During this period the spider was extremely active for a guarding individual (see Morse 1987). It moved to the top of its nest and subsequently changed position 14 times over the next 30 min. These movements included both shifts between the underside and upperside, and between the petiole of the nest leaf and the nest at the terminal end of this leaf. This rate is eight times greater than that of average guarding spiders at other times. ($\bar{X} \pm \text{SD} = 3.3 \pm 3.8$ moves/h, virtually all associated with nest maintenance; $N = 34$; Morse, unpublished data), and twice the rate of the most active guarding *Misumena* I have monitored.

Approximately 30 minutes from the beginning of these observations, the ichneumon walked to the upper surface of the nest from the leaf it had previously used. At this time the spider occupied the upper surface of its nest, on the distal end of the leaf. As the wasp neared the nest from the proximal end, the spider instantly became active. It approached and attacked the wasp, seemingly as it would attack a prey item, raising its front pairs of legs and striking down on it. However, the spider did not bite the wasp; instead, it flung the wasp from the nest toward the ground. The wasp landed on my trousers leg, a few cm distal to the nest leaf and about 30 cm below the nest. It remained there for one minute, behaving as it did on the originally-occupied leaf, largely stationary, but regularly moving its antennae. Perhaps this initial action would normally have sufficed to remove the wasp from the vicinity of the nest. I then picked the wasp up on a blade of grass and placed it back on the spider's upper nest surface. The spider again quickly attacked, but this time it only displaced the wasp 2-3 cm; the wasp landed on the extreme distal end of the nest following this attack. Instantly the wasp moved to the side of the nest and walked rapidly along the side, probing several times with its ovipositor. Post-reproductive spiders draw the upper and lower parts of their nests together tightly with silk; but this junction might nevertheless provide the most satisfactory place to insert an ovipositor. An ovipositor thrust into the top or bottom of the nest would penetrate the milkweed leaf, and thus run the risk of becoming clogged by milkweed latex (see Dussourd and Eisner 1987).

The spider attacked the wasp in a similar way on the side of the nest, but ineffectually, for the wasp merely retreated to the other side of the nest and probed there with its ovipositor. The spider moved toward the wasp once again, but the wasp ran directly over the spider and across the dorsal side of the nest, with its ovipositor pointed downward. The spider was on the opposite side of the nest at this time. The wasp again moved to the side of the nest and inserted, or attempted to insert, its ovipositor between the upper and lower layers of the nest. After this action, it moved to the leaf it had occupied at the beginning of the observations. During this entire period it did not fly. After it had remained largely inactive on its original site for 10 minutes, I again placed it on the spider's nest, and the spider once more attacked it. The wasp retreated this time, and moved to another adjacent leaf. I then attempted to place the wasp on another spider's nest, but upon being placed there, it flew for the first time, and I soon lost sight of it.

Given the aggressive response of the spiders, it may seem surprising that the second spider did not kill the wasp. This initial aggressive response was similar to the one I have observed when these spiders attack other hymenopterans. Since I have seen even post-reproductive *Misumena* with yellowjacket (*Vespula* sp.) kills (Morse 1987), they must be capable of penetrating *Trychosis*' carapace. Further, both pre- and post-reproductive *Misumena* regularly take small euminid wasps, insects of a comparable size and carapace hardness to *Trychosis*. Although reproductive spiders do not actively seek food, some of them do capture occasional insects that approach them while they guard their nests (Morse 1987).

The initial response of the spiders may typically suffice to dissuade these egg predators, as the first wasp's behavior suggests. Further, physically displacing *Trychosis* from the nest may normally keep it from attacking again. Askew (1971) notes that caterpillars may regularly elude ichneumonid parasitoids by descending from a leaf on a thread, and that ichneumonid pupae may themselves escape pteromalid hyperparasites by dropping into the substrate. These observations suggest that some hymenopterans are not highly skilled at tracking mobile targets; perhaps they also experience difficulty in relocating a stationary target from which they have been displaced.

The interactions at the second nest suggest a possible explanation for the difference in predation levels on the egg masses of large and small spiders. The large spiders may on average be more successful in quickly removing the wasps from their nests than are the small spiders. Subsequent efforts of the spider at the second nest became progressively less effectual.

Nevertheless the ichneumonid did not successfully attack the second nest, because no wasp offspring emerged. I could not determine whether the wasp actually laid an egg, however. It may require a minimum period on the nest to determine whether the nest is a satisfactory egg-laying site. The fact that the first wasp visited a nest probably far too old for it to exploit suggests that *Trychosis*' initial level of discrimination is low.

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BOOK REVIEWS

Roberts, M. J. 1987. The Spiders of Great Britain and Ireland. Harley Books, Martins, Great Horkesley, Colchester, Essex, CO6 4AH England. Vol. 2 (Linyphiidae) (Price £45.00).

The first and third volume of this three volume work were reviewed by B. J. Kaston in this Journal (Vol. 13, no. 2, pp. 275-276) in 1985. Volume two has now been published, and includes descriptions and illustrations of 267 species of linyphiids, placed in 105 genera. There is also an addendum listing six nonlinyphiid spiders new to Great Britain, a page and half illustrating variation in *Araneus diadematus*, a glossary, a checklist of British spiders, and an index to scientific names.

The short key segregates the linyphiid species into four groups on the basis of tibial spines and metatarsal trichobothria. The key is followed by four tables, one for each group, listing genera and species and comparing the general appearance, total length of the specimens, positions of the trichobothria and tibial spines, with reference to the text figures. It is hoped that the key and tables, with the help of the illustrations, will guide the reader to a correct determination.

The volume is lavishly illustrated. For most species, one page has the species name, references to illustrations, plus a few lines of description, and the illustrations are on the facing page. A paragraph under the last species of each genus summarizes the distinguishing characters of the species included within the genus, while another paragraph summarizes distribution and habitats. There are no literature citations other than the original description of the species.

The epigynes are illustrated next to the palpi, with views of carapaces on a separate page. Unlike the previous volumes, Volume 2 has all illustrations to the same scale, genitalia 90X, carapaces 60X. Thus many illustrations are of magnificent size, while illustrations of smaller species may be barely visible. Many illustration pages show an unusual amount of blank space due to the minute size of the species and illustrations.

There are several ways to illustrate spider genitalia. In North America illustrations are prepared using reflected light at the time the genitalia are examined. Much less satisfactory are illustrations of genitalia mounted on a microscope slide and examined by transmitted light. Slide mounted palpi are difficult to place in comparable positions, they may be compressed, they deteriorate rapidly (when not dismounted), and often such slides become separated from the specimen. Unfortunately, however, this method is popular because compound microscopes are more readily available than stereoscopic dissecting microscopes. The third and most modern method for illustrating spider genitalia is by use of the scanning electron microscope (SEM). While SEMs show minute details of surface sculpturing, and may be extraordinarily interesting and valuable, it is difficult to use this method for comparison with specimens to be keyed out. Roberts has illustrated with reflected light, the best method for the

purpose. Often two or more epigyna are illustrated for the same species, showing individual differences due to variable transparency of the surface. It might have been more useful if Roberts had provided only one illustration of an unprepared epigynum and, for the second, had used a cleared epigynum, showing the underlying ducts.

This new volume should be compared with its counterpart, vol. 2 of Locket, G. H. and A. F. Millidge's *British Spiders*, Ray Soc. 1953. Millidge illustrated only 250 species, included a key to linyphiid genera (but not to species) and gave citations for species in addition to the original ones. Roberts' illustrations usually show much more detail, especially of the epigyna. However, Robert's illustrations of small species are smaller than those by Millidge. If there was criticism of Millidge's work, it was that illustrations of epigyna, palpi and carapaces of the same species were often on separate pages and that the palpi were all illustrated in retrolateral (lateral) view. While the lateral view may give most diagnostic characters for the limited fauna of the British Isles, it makes their interpretation impossible for an outsider who wants to study the palpus of a given genus; for this purpose, a ventral view would be needed in addition to the lateral. This limitation makes Millidge's illustrations frustrating to use for North American or Holarctic species that need to be placed into genera. Unfortunately Roberts illustrates the same lateral view of the palpus that Millidge used, albeit with greater detail and, in the larger illustrations, finer craftsmanship (however, some small illustrations show less detail). Millidge's treatment frequently gives a second illustration of the palpal tibia to assist the identification, but there is only one palpus illustration in Roberts' volume.

In summary: this is a superb, authoritative volume. Perhaps inevitably, it will be more useful to those working with the British fauna than to those who want to increase their understanding of linyphiid spiders of the world.

Herbert W. Levi, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138 USA.

Eberhard, W. G., Y. D. Lubin and B. C. Robinson (Eds.). 1986. *Proceedings of the Ninth International Congress of Arachnology*, Panama 1983. Smithsonian Institution Press, Washington, DC. 334 pp. (Price \$25).

One of the most difficult tasks a reviewer can be assigned is the evaluation of a proceedings volume from a general meeting. There is no unifying theme in such a book except for the limitations on the membership of the sponsoring group (here all the papers concern arachnids, though insects are the real focus of at least two of them). The erratic quality of the short papers, many serving as abstracts of a more complete article published elsewhere, is particularly obvious when there has been no pre-presentation screening.

It will come as no surprise to those who have read several such volumes that a small number of the papers probably could not have been published in a reviewed journal. The less said about these efforts, the better. The largest class of papers consists of reports of the smaller byways and peculiar backwaters explored during the author's main research efforts, or first attempts by students, or, sad to say,

the same paper presented at the previous meeting, or the one before that, with a few cosmetic alterations. A majority of the papers in this volume, however, are interesting and valuable nonetheless.

Bleckmann (p. 19) presents an elegant analysis of the response of *Dolomedes* spiders to surface waves on water, showing how the spiders discriminate waves caused by prey and extract a surprising amount of information from them. For me, this was the outstanding paper in the volume.

New behavioral phenomena and new structures connected with them are reported in the papers by Coyle (p. 33) on mating in *Euagrus* (the males use a patch of spines that functions like Velcro™) and by Robinson, Robinson, Murphy, and Corley on egg-sac burying by *Nephila maculata*. These papers are refreshingly original and well written and illustrated. Edmunds (p. 61) uses a detailed study on the stabilimentum in two species of *Argiope* to review stabilimentum function and evolution in orb weavers in general, concluding, sensibly, that stabilimentum function may vary from species to species.

In the area of systematics and biogeography, van Helsdingen's (p. 121) survey of the world distribution of Linyphiidae provides an important data base and should set the course of systematic research in this neglected family for some time to come. Quintero (p. 203) presents a new classification of Amblypygi which may prove controversial but which is well argued and amply illustrated. Finally, Raven (p. 223) summarizes his new treatment of the mygalomorphs, the details of which have now been published elsewhere.

The editing of this volume, unfortunately, leaves much to be desired, but primarily on the technical side—there should have been more careful proofreading. It is particularly bothersome to have obvious typographical errors in the boldface titles of articles. For example, on p. 301, the word "Summary" is treated as if it were the name of the author of a species. On p. 320 we see "Hersilidae" instead of Hersiliidae. On p. 332, "*Argiope bruennichii*" is given as the name of a coauthor of a paper. Even in the table of contents one finds words like "umarobiid." Throughout there is erratic application of the convention of putting species names in italics, including one of the papers by the senior editor. A few of the illustrations (see pp. 183 and 186) are not of publishable quality but the blame here must be shared with the authors. An organization of the papers and abstracts into biological categories would have been preferable to publishing them in alphabetical order by the author's last name.

However, the price of the volume is reasonable and the majority of the papers are worth reading. Despite the several sour chords struck in the paragraphs above, I recommend that professionals in the field add it to their personal libraries.

I also recommend that in future such volumes not be published. The required limitations on the included papers, their erratic quality, the tantalizing nature of abstracts that stand alone (and in several cases, as of this writing, reports abstracted in this book have not yet appeared, some four years later), are significant shortcomings. Add to this the difficulties of finding such "one-shot" volumes in libraries.

Of the three congresses or meetings I attended in 1987, the most valuable (a Smithsonian-sponsored conference on the evolution of terrestrial ecosystems) banned the presentation of papers and instead organized the participants into overlapping working groups charged with summarizing the past, present, and

future of an area of research in an informal report. How much more refreshing and stimulating it would be if the participants in congresses and meetings simply discussed their current research in a less formal, more open, and speculative fashion, without the constraints of having to present a finished paper for publication. I vote for talks about research in progress, followed by vigorous discussion, rather than formal papers on last year's results!

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Cover photograph, spider figure on men's meeting house, Palau, by J. W. Berry

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Viera, V. y F. G. Costa. 1988. Analisis del comportamiento de captura de presas por machos adultos de *Metepeira* sp. A (Araneae, Araneidae), utilizando telas de juveniles y hembras adultas coespecificos. J. Arachnol., 16:141-152.

ANALISIS DEL COMPORTAMIENTO DE CAPTURA DE PRESAS POR MACHOS ADULTOS DE *METEPEIRA* SP. A (ARANEAE, ARANEIDAE), UTILIZANDO TELAS DE JUVENILES Y HEMBRAS ADULTAS COESPECIFICOS

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ABSTRACT

Prey (*Acromyrmex* sp. ants) were offered to four experimental groups of *Metepeira* sp. A: adult females on their own webs; juveniles on their own webs; adult males on webs built by adult females; adult males on webs built by juveniles. Although adult males do not build webs, they are fully capable of capturing prey in foreign webs. Male behavior was basically similar to females and juveniles. However, males showed high frequency in certain units of behavior in the prey detection phase (particularly males on female webs). A sexual origin for these units of behavior is suggested. Sexual interference would reduce the predatory efficiency of males but also probably reduce the risk of female predation on males in the field.

RESUMEN

Se entregaron presas (hormigas *Acromyrmex* sp.) a cuatro grupos experimentales de *Metepeira* sp. A: hembras adultas ocupando sus telas; juveniles ocupando sus telas; machos adultos ocupando telas de hembras; machos adultos ocupando telas de juveniles. Los machos adultos, que no construyen telas orbiculares, mostraron plena habilidad predatoria en telas ajenas. El comportamiento de los machos fue básicamente similar a hembras y juveniles. Sin embargo, los machos presentaron alta frecuencia de algunas unidades de comportamiento en la fase de detección (principalmente machos en telas de hembras). Se sugiere un origen sexual de estas unidades. Esta característica afectaría la eficiencia de captura pero disminuiría los riesgos de predación sobre los machos en el campo.

INTRODUCCION

Los machos adultos de Araneidae pierden la capacidad de construir telas orbiculares a partir de su muda de maduración y consecuentemente no se alimentarían (Bristowe 1941; Millot 1949; Foelix 1982). Sin embargo, en especies de *Nephila* y *Argiope*, los machos son mucho más pequeños que las hembras, ocupan y eventualmente se alimentan en telas de hembras adultas o en penúltimo estadio (Christenson y Goist 1979; Robinson y Robinson 1978; Vollrath 1980; Christenson 1984; Christenson et al. 1985). En *Eriophora fuliginea* (C. L. Koch) los machos tienen un tamaño similar a las hembras, construyen redes orbiculares y capturan presas (Robinson et al. 1971; Robinson y Robinson 1981). Eberhard et al. (1978) señalaron robos de telas de *Metazygia gregalis* (O.P.-Cambridge) por

machos adultos de varias especies orbitelares, incluyendo machos coespecíficos, utilizándolas para capturar presas. Pese a estos antecedentes, no se conocen descripciones detalladas del comportamiento de captura de presas por machos adultos de Araneidae.

Las telas de las especies de *Metepeira* se caracterizan por la presencia de un refugio y de hilos de conexión con el centro de la tela orbicular. Los machos adultos tienen un tamaño semejante a las hembras y pueden utilizar telas ajenas para capturar presas. Por ejemplo, los machos de *M. grinnelli* (Coolidge) pueden desplazar a individuos de *Cyclosa turbinata* (Walckenaer), ocupar sus telas y capturar presas (Spiller 1984). También los machos adultos de *Metepeira* sp. A ocupan y capturan presas en telas de juveniles y hembras coespecíficos (Viera y Costa 1985). Este último resultado nos estimuló a averiguar si el comportamiento de captura de presas de los machos adultos de esta especie es similar al descrito por Viera (1986) para los juveniles y las hembras adultas.

Los objetivos de este trabajo son: (i) Describir el comportamiento de captura de presas por machos adultos de *Metepeira* sp. A ubicados en telas de juveniles y hembras coespecíficos; (ii) Describir el comportamiento de captura de presas por juveniles y hembras adultas de *Metepeira* sp. A (grupos de control); (iii) Analizar comparativamente los comportamientos de captura de juveniles, hembras, machos en telas de juveniles y machos en telas de hembras, sobre una misma presa.

Este estudio constituye el primer intento de analizar el modelo comportamental de captura de presas, realizado por machos adultos de Araneidae. Los resultados también permitirán evaluar la capacidad depredadora de los machos y la influencia del tipo de tela utilizada, así como vincular esta actividad alimentaria con las tácticas reproductoras de Araneidae.

MATERIAL Y METODO

Se colectaron 145 individuos juveniles y adultos de *Metepeira* sp. A (denominación provisoria, sugerida por H. W. Levi, Harvard University) en Punta Espinillo, Montevideo, Uruguay. Las telas fueron localizadas en inflorescencias y parte superior del tallo de *Eryngium* sp. (Umbelliferae), con el refugio ubicado generalmente entre la umbela y el pedicelo (hasta cinco telas en el mismo tallo). Todos los individuos utilizados fueron depositados en la colección aracnológica del Museo Nacional de Historia Natural, Montevideo (lote N° 305).

En el laboratorio los individuos fueron criados en frascos individuales de 9 cm de diámetro y 14 cm de altura, con un recipiente con agua y un soporte para la tela, cerrados con una malla de nailon. Fueron alimentados con larvas de *Tenebrio* sp. (Coleoptera). La temperatura media durante 166 días de cría y estudio fue $22.96 \pm 1.95^{\circ}\text{C}$. Para las experiencias los individuos se trasladaron a cajas de vidrio de $30 \times 30 \times 9$ cm, con un marco interno de madera y un recipiente con agua. Las arañas que mudaron se usaron después de cinco días. Las presas elegidas fueron obreras de *Acromyrmex* sp. (Hymenoptera, Formicidae) con fuertes defensas mecánicas y muy abundantes en el sitio de colecta. El tamaño de la presa fue igual o ligeramente inferior a la araña, ubicándola en la zona inferior de la tela, 2 h después de su captura. Para la observación se utilizó un fondo oscuro, una luz puntiforme lateral de 445 lux y una lupa amplia de 2X. Se relataron y registraron las observaciones con un grabador magnetofónico, se filmaron algunas secuencias con una cámara

cinematográfica Super-8 y se analizaron cuadro a cuadro en una moviola. Las secuencias comportamentales se describieron separando unidades y fases comportamentales de acuerdo a Robinson y Olazarri (1971) y particularmente Viera (1986).

El diseño experimental fue el siguiente: *Experiencia 1*: Se colocaron hembras adultas individualmente en los recipientes de experimentación limpios. A las 24 ó 48 h se entregó la presa a las arañas que construyeron tela y se observó y registró la captura. *Experiencia 2*: Se colocaron machos adultos en recipientes de experimentación inmediatamente después de ser extraídas las hembras adultas (sin alterar la tela). Veinticuatro horas después se controló la ocupación de la tela por el macho, se entregó la presa y se observó y registró la captura. *Experiencia 3*: Se siguió el mismo procedimiento de la Experiencia 1, pero usando juveniles (en penúltimo y antepenúltimo estadios) en sustitución de las hembras. *Experiencia 4*: Se siguió el mismo procedimiento de la Experiencia 2, pero colocando machos en telas construídas por individuos juveniles.

Las observaciones correspondientes a las cuatro experiencias se realizaron intercaladas entre sí. Se registraron las experiencias desde el momento de colocar la presa (*inicio*). Las sucesiones de unidades se contabilizaron a partir de la primera unidad de comportamiento que se observó después de entregar la presa, exceptuando el reposo anterior de la araña. Se consideró como *fin* de las experiencias la ingestión o abandono de la presa, así como también el mantenimiento de quietud o acicalamiento por un lapso mayor a 60 seg. La eficiencia de captura se calculó: $(N^{\circ} \text{ de presas capturadas} / N^{\circ} \text{ de presas entregadas}) \times 100$. La temperatura media durante las observaciones experimentales fue: $23.3 \pm 2.3^{\circ}\text{C}$ ($N = 78$). Los resultados obtenidos de las cuatro experiencias se compararon cualitativamente y cuantitativamente. No se compararon entre sí las experiencias 1 y 4, ni las experiencias 2 y 3, para evitar la incidencia simultánea de dos variables (estado fisiológico y medio ambiente experimental). Se utilizaron los estadísticos: test de probabilidad exacta de Fisher, test de dos muestras de Wilcoxon (Siegel 1956) y test de diferencia de medias de Student con restricciones para la varianza (paquete PRESTA, Centro S. Ramón y Cajal, España). El nivel mínimo para rechazar la hipótesis nula fue 0.05.

RESULTADOS

El comportamiento de captura en los cuatro grupos experimentales mostró un patrón común, donde las unidades de comportamiento se sucedieron en el tiempo. De acuerdo con Viera (1986), se reconocieron tres fases: (1) *Fase de detección de la presa*, constituída por las unidades desplazamiento (locomoción de la araña en la tela), tensamiento (tironeo de los radios de la tela) y toqueteo (golpes suaves de patas sobre la presa); (2) *Fase de inmovilización de la presa*, constituída por las unidades envolvimiento (sujeción con ataduras de seda), mordeduras cortas (inserciones sucesivas de los quelíceros en la presa) y mordedura prolongada (inserción de los quelíceros en la presa durante 20 segundos como mínimo); (3) *Fase terminal*, constituída por las unidades transporte (liberación y traslado de la presa en las patas IV hasta el lugar de ingestión) y manipulación de la presa (maniobras de ubicación de la presa, previas a la ingestión).

Se observaron otras dos unidades: quietud (inmovilidad total) y acicalamiento (limpieza aparente de los apéndices). Quietud se vinculó frecuentemente con la fase inmovilización y acicalamiento se vinculó con detección e inmovilización.

Sucesión de unidades de comportamiento de hembras (Experiencia 1).—De 21 hembras empleadas, 19 hicieron tela. Diecisiete iniciaron la captura desplazándose hasta el centro de la tela (Fig. 1), mientras que dos hembras partieron desde el centro de la tela (una de éstas no construyó refugio). Desde el centro todos los individuos se desplazaron directamente hacia la presa, salvo uno que previamente realizó tensamiento. Un sólo individuo efectuó toqueteo sobre la presa, después del desplazamiento inicial.

Dieciocho individuos envolvieron la presa inmediatamente después de desplazarse. La fase inmovilización mostró una fuerte vinculación entre envolvimiento y mordeduras cortas. Ambas unidades se vincularon en menor medida con mordedura prolongada (Fig. 1).

La fase terminal se inició con la unidad transporte, sucediendo a envolvimiento, mordedura prolongada o excepcionalmente mordeduras cortas (2 individuos). Diecisiete hembras presentaron fase terminal e ingirieron en el refugio; dos hembras no realizaron fase terminal y finalizaron el comportamiento en quietud.

Quietud se relacionó fundamentalmente con envolvimiento; también se vinculó con mordedura prolongada, mordeduras cortas, acicalamiento y transporte. Acicalamiento se observó repetidamente en un sólo individuo, relacionado con envolvimiento y quietud.

La eficiencia de captura de presas fue 95% (un sólo individuo no capturó la presa).

Sucesión de unidades de comportamiento de machos que utilizaron telas de hembras (Experiencia 2).—De 18 machos empleados, 17 ocuparon telas de hembras. Quince individuos iniciaron el comportamiento de captura desde el refugio y dos desde el centro de la tela (una tela no poseía refugio). Once machos realizaron como primera unidad desplazamiento y seis tensamiento (Fig. 2). Ocho machos realizaron tensamiento y 10 machos realizaron toqueteo durante la fase detección de la presa.

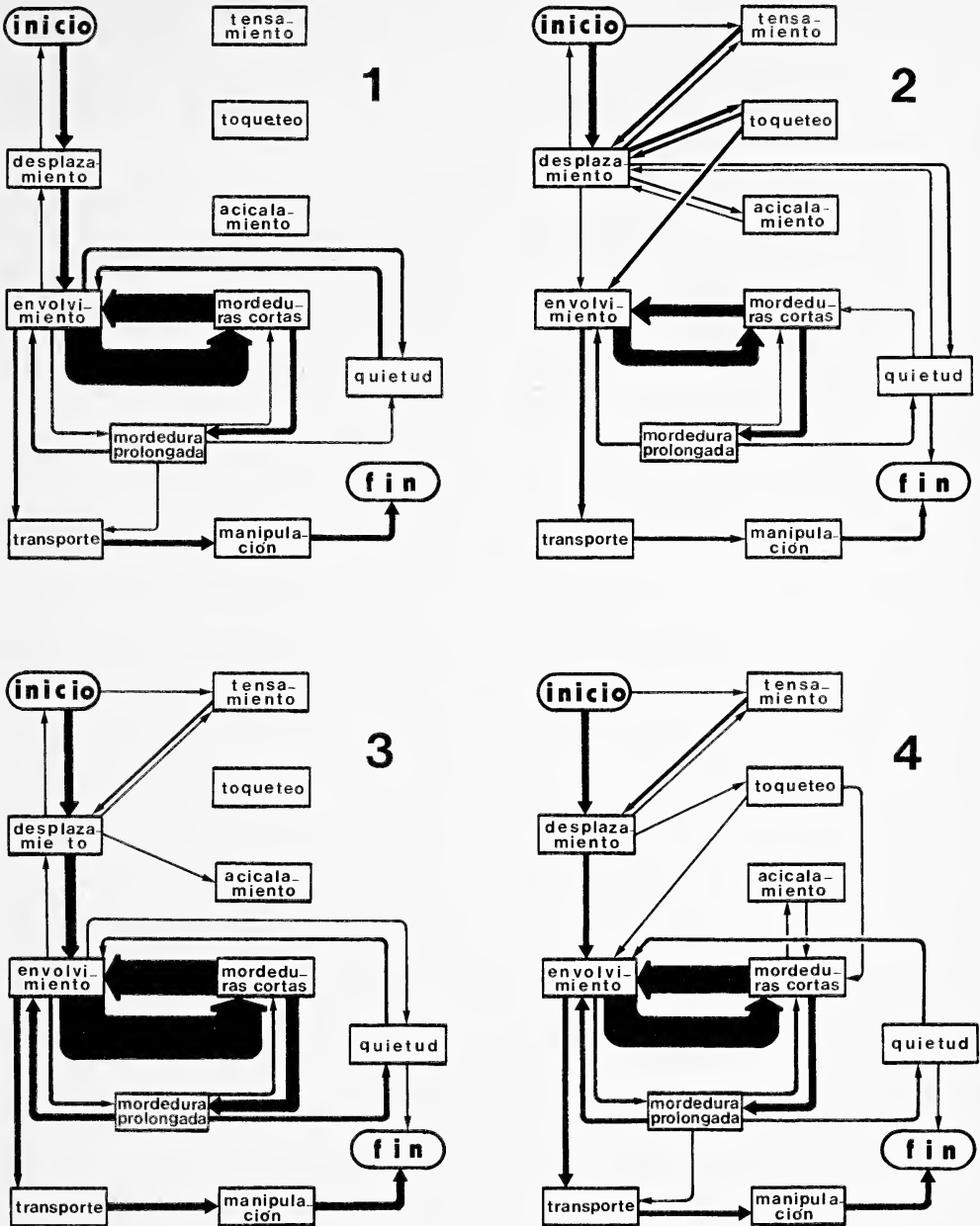
La fase inmovilización se inició con las sucesiones desplazamiento a envolvimiento o toqueteo a envolvimiento. Envolvimiento se relacionó estrechamente con mordeduras cortas y ambas unidades se vincularon con mordedura prolongada (Fig. 2).

Ocho machos comenzaron la fase terminal con la sucesión envolvimiento a transporte y un individuo con la sucesión mordedura prolongada a transporte. Quietud se vinculó con mordeduras cortas y mordedura prolongada.

Cinco individuos terminaron el comportamiento realizando quietud (dos de ellos ubicados en el refugio) y uno desplazándose fuera de la tela. Acicalamiento fue observado en cinco individuos, relacionándose principalmente con desplazamiento y en menor medida con quietud, envolvimiento y tensamiento. Un individuo terminó su comportamiento en acicalamiento prolongado.

La eficiencia de captura de presas fue 72% (cinco machos no capturaron las presas).

Sucesión de unidades de comportamiento de juveniles (Experiencia 3).—De 32 juveniles empleados, 24 hicieron tela (siete de ellos eran machos penúltimos). Una tela se destruyó accidentalmente, previo a la observación. Diecinueve juveniles se



Figs. 1-4.—Sucesiones de unidades de comportamiento observadas en la captura de hormigas (*Acromyrmex* sp.) en cuatro grupos experimentales de *Metepeira* sp. A. Las unidades de comportamiento se sucedieron excluyéndose entre sí en el tiempo; las frecuencias de sucesión entre estas unidades se indicaron con el espesor de las flechas (1 mm-10 sucesiones); las frecuencias iguales o menores al 10% del número de observaciones no fueron dibujadas, a efectos de facilitar la comparación visual: 1, diagrama de frecuencias de 19 hembras adultas en sus propias telas (Experiencia 1); 2, diagrama de frecuencias de 17 machos adultos ocupando telas de hembras adultas (Experiencia 2); 3, diagrama de frecuencias de 23 juveniles en sus propias telas (Experiencia 3); 4, diagrama de frecuencias de 19 machos adultos ocupando telas de juveniles (Experiencia 4).

observaron inicialmente en el refugio y cuatro en el centro de la tela. Veintiún individuos iniciaron su actividad con desplazamiento y dos con tensamiento. Tensamiento se vinculó principalmente con desplazamiento y una única vez con toqueteo. Toqueteo se relacionó además con mordeduras cortas, envolvimiento, desplazamiento, transporte y quietud.

Todos los individuos comenzaron la fase inmovilización con envolvimiento, que se vinculó estrechamente con mordeduras cortas. Ambas unidades se vincularon en menor medida con mordedura prolongada. Mordedura prolongada se relacionó fundamentalmente con mordeduras cortas (Fig. 3).

Catorce individuos comenzaron la fase terminal desde la unidad envolvimiento, dos después de mordedura prolongada, dos después de mordeduras cortas y uno después de quietud. Dieciseis juveniles desarrollaron íntegramente la fase terminal, ingiriendo en el refugio.

Quietud se vinculó principalmente con mordedura prolongada y envolvimiento, relacionándose con menor frecuencia con transporte, mordeduras cortas, toqueteo, desplazamiento y acicalamiento. Seis individuos terminaron el comportamiento en quietud. Acicalamiento fue realizado por tres individuos y se relacionó principalmente con desplazamiento y en menor medida con envolvimiento, quietud, transporte y manipulación. Un macho subadulto abandonó la presa después de inmovilizarla y terminó su comportamiento realizando acicalamiento. No se observaron otras diferencias entre los machos subadultos y los otros juveniles.

La eficiencia de captura de presas fue 100%.

Sucesión de unidades de comportamiento de machos que utilizaron telas de juveniles (Experiencia 4).—De 23 machos empleados, 19 ocuparon telas: 14 se ubicaron en el refugio y cinco en el centro de la tela. Quince individuos realizaron inicialmente desplazamiento y cuatro comenzaron con tensamiento. Seis machos realizaron tensamiento y nueve toqueteo en la fase detección (Fig. 4).

El pasaje de la fase detección a la fase inmovilización se realizó con las sucesiones desplazamiento a envolvimiento o toqueteo a envolvimiento. La fase inmovilización presentó también una fuerte relación entre envolvimiento y mordeduras cortas. Ambas unidades se vincularon en menor medida con mordedura prolongada (Fig. 4).

La fase terminal fue realizada por 15 individuos: 11 a partir de envolvimiento y cuatro a partir de mordedura prolongada. Cuatro machos terminaron el comportamiento en quietud; uno de ellos abandonó la presa una vez inmovilizada.

Quietud se vinculó principalmente con envolvimiento y mordedura prolongada y en menor medida con toqueteo, desplazamiento, mordeduras cortas y transporte. Acicalamiento se relacionó fundamentalmente con mordeduras cortas, toqueteo y envolvimiento.

No se observaron diferencias entre machos que ocuparon telas de machos subadultos y machos que ocuparon telas de otros juveniles.

La eficiencia de captura de presas fue 95% (un sólo macho no capturó la presa).

Comparación entre los grupos experimentales.—Se compararon estadísticamente las frecuencias absolutas de unidades de comportamiento entre: (i) Experiencia 1 y Experiencia 2; (ii) Experiencia 3 y Experiencia 4; (iii) Experiencia 1 y Experiencia 3; (iv) Experiencia 2 y Experiencia 4. Las unidades de

comportamiento cuyas frecuencias fueron menores al número de observaciones (no presentes en todas las observaciones), se compararon mediante el test de Fisher y las unidades de frecuencia mayor o igual al número de observaciones (presentes en todas las observaciones) se compararon mediante el test de Wilcoxon. Las duraciones de las fases comportamentales se compararon mediante el test de Student.

a. Comparaciones mediante el test de Fisher: Se compararon las frecuencias de las unidades tensamiento, toqueteo, acicalamiento, transporte, manipulación y quietud, como también la frecuencia de captura en los cuatro grupos experimentales (Tabla 1). La unidad tensamiento mostró diferencias significativas entre las experiencias 1 y 2, reflejando la mayor frecuencia presentada por los machos de la Experiencia 2. La unidad toqueteo mostró diferencias en dos comparaciones (Tabla 1), presentando frecuencias altas en los dos grupos de machos (experiencias 2 y 4). Acicalamiento se observó con alta frecuencia también en machos, pero se observaron diferencias significativas sólo en la comparación Experiencia 1-Experiencia 2. Las hembras mostraron una alta frecuencia en las unidades transporte y manipulación (fase terminal), presentando diferencias significativas con los machos de la Experiencia 2. La baja frecuencia de estos últimos determinó también diferencias en la unidad transporte con los machos de la Experiencia 4. La unidad quietud no mostró diferencias estadísticas entre los grupos, aunque se observó una frecuencia alta en los juveniles.

La eficiencia de captura de presas fue máxima en los juveniles, alta en hembras y machos de la Experiencia 4 y baja en los machos de la Experiencia 2. Se diferenció estadísticamente la frecuencia de captura de hembras con los machos de la Experiencia 2 (Tabla 1).

b. Comparaciones mediante el test de Wilcoxon: Se compararon las frecuencias de las unidades desplazamiento, envolvimiento, mordeduras cortas y mordedura prolongada en los cuatro grupos experimentales (Tabla 2). No se encontraron diferencias estadísticamente significativas en las frecuencias de las unidades desplazamiento y mordedura prolongada. Los machos de la Experiencia 2 presentaron frecuencias bajas en envolvimiento y mordeduras cortas, que resultaron distintas estadísticamente respecto a hembras y machos de la Experiencia 4.

c. Comparaciones generales de frecuencias: Los cuatro grupos experimentales presentaron un patrón común del comportamiento de captura sobre *Acromyrmex* sp., constituido por tres fases que se suceden en el tiempo. Los modelos de captura de hembras y juveniles fueron indistinguibles entre sí a la luz de las comparaciones efectuadas, no presentando diferencias significativas en las frecuencias de unidades ni en la frecuencia de captura. Los juveniles se diferenciaron de los machos que capturaron en las mismas telas (Experiencia 4) solamente en la frecuencia de toqueteo. Los dos grupos de machos presentaron una fase detección más compleja que hembras y juveniles, accediendo a la fase inmovilización no sólo desde desplazamiento sino también desde toqueteo (Figs. 2 y 4). Los machos de la Experiencia 2 presentaron diferencias en las frecuencias de tres unidades de comportamiento respecto a los machos de la Experiencia 4, mientras que se diferenciaron en las frecuencias de siete unidades y en la captura de presas con las hembras (Tablas 1 y 2). Para tener una idea global comparativa de los cuatro grupos experimentales, se sometieron los valores de frecuencias de unidades a técnicas de agrupamiento. La Fig. 5 permite destacar nuevamente la

Tabla 1.—Comparaciones entre las frecuencias de unidades de comportamiento y de captura de la presa en los cuatro grupos experimentales, utilizando el test de probabilidad exacta de Fisher (* = diferencias significativas).

| UNIDADES | Exp. 1-Exp. 2 | Exp. 3-Exp. 4 | Exp. 1-Exp. 3 | Exp. 2-Exp. 4 |
|---------------|--------------------------|---------------|---------------|---------------|
| Tensamiento | 0.016* | 0.248 | 0.146 | 0.174 |
| Toqueteo | 6.150×10^{-4} * | 0.015* | 0.301 | 0.209 |
| Acicalamiento | 0.028* | 0.327 | 0.301 | 0.127 |
| Transporte | 0.016* | 0.219 | 0.146 | 0.039* |
| Manipulación | 0.016* | 0.222 | 0.146 | 0.075 |
| Quietud | 0.261 | 0.089 | 0.136 | 0.247 |
| Captura | 0.016* | 0.452 | 0.198 | 0.060 |

disimilitud de los machos de la Experiencia 2 respecto a los otros grupos, que son muy similares entre sí.

d. Duración de las fases comportamentales:—Los resultados obtenidos del registro temporal del comportamiento de los cuatro grupos experimentales se exponen en la Tabla 3. Se destaca una gran dispersión de todos los valores. Se compararon estos valores en los distintos grupos experimentales mediante el test de diferencia de medias de Student con restricciones para la varianza. Los resultados no mostraron diferencias estadísticamente significativas en las fases inmovilización y terminal, ni en la duración total del comportamiento de captura; se observaron sí diferencias en la fase detección en las hembras respecto a los machos de la Experiencia 2 y los juveniles (Tabla 4). Estos resultados reflejan la corta duración de esta fase en las hembras. Los machos de la Experiencia 2 mostraron una fase detección sumamente extensa y a la vez la máxima variabilidad.

e. Reparación de la tela:—Aunque no se controlaron metódicamente todas las observaciones, se observó que hembras y juveniles repararon siempre la tela después de la captura, mientras que los machos de las experiencias 2 y 4 no repararon nunca la tela.

DISCUSION

En el campo (Punta Espinillo) los autores observaron machos adultos de *Metepeira* sp. A ocupando telas orbiculares aparentemente coespecíficas, capturando presas (cinco observaciones). En el laboratorio, los machos adultos de esta especie no construyen telas orbiculares, ocupan telas de juveniles y hembras adultas coespecíficos y capturan presas, sin reparar las telas (Viera y Costa 1985).

Tabla 2.—Comparaciones entre frecuencias de unidades de comportamiento en los cuatro grupos experimentales, utilizando el test de Wilcoxon (* = diferencias significativas).

| UNIDADES | Exp. 1-Exp. 2 | Exp. 3-Exp. 4 | Exp. 1-Exp. 3 | Exp. 2-Exp. 4 |
|----------------|----------------------|---------------|------------------|---------------------|
| Desplazamiento | $P > 0.1$ | $P > 0.1$ | $P > 0.1$ | $P > 0.1$ |
| Envolvimiento | $0.01 > P > 0.002$ * | $P > 0.1$ | $P > 0.1$ | $0.05 > P > 0.01$ * |
| Mordeduras | | | | |
| cortas | $0.05 > P > 0.01$ * | $P > 0.1$ | $P > 0.1$ | $0.05 > P > 0.01$ * |
| Mordedura | | | | |
| prolongada | $P > 0.1$ | $P > 0.1$ | $0.1 > P > 0.05$ | $P > 0.1$ |

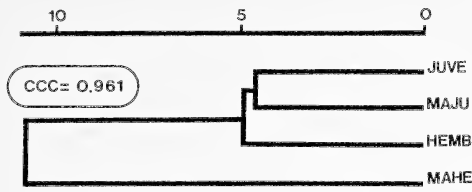


Fig. 5.—Fenograma de los cuatro grupos experimentales (OTUs) en base a las frecuencias absolutas de 10 unidades de comportamiento (caracteres). Coeficiente de distancia de Crovello, UPGMA y técnica de ligamiento promedio. HEMB = hembras en sus telas; MAHE = machos en telas de hembras; JUVE = juveniles en sus telas; MAJU = machos en telas de juveniles.

Los resultados del presente trabajo muestran que los machos de esta especie mantienen intacto el patrón de captura de los estadios juveniles, inmovilizando las presas con seda y transportándolas al refugio. También se observaron, en los machos, elementos motores particulares (cualitativa y cuantitativamente) probablemente vinculados con el comportamiento sexual. Los resultados de las experiencias de control (captura por hembras adultas y por juveniles) coincidieron básicamente con la descripción de Viera (1986).

Sin embargo, deben destacarse algunas diferencias entre resultados anteriores (Viera 1986) y los del presente estudio, respecto a la predación de hembras y juveniles: (i) Viera describió una fase de detección compleja (desplazamiento 1—orientación—desplazamiento 2) que en el presente trabajo se observó simplificada (desplazamiento). Esta diferencia respondería a que en el presente trabajo la presa se ubicó en la vertical inferior de la tela y resultó inaparente la orientación de la araña en el centro de la tela; (ii) Viera observó sólo un caso de acicalamiento (4%) y aquí se observaron siete casos (17%); (iii) toqueteo se vinculó aquí con detección y en Viera con la fase inmovilización de la presa. Estas dos últimas diferencias pueden ser debidas al azar o reflejar diferencias no controladas en el método. Las diferencias entre los trabajos señalan también la conveniencia del uso metódico de grupos de control.

El comportamiento de captura realizado por hembras fue similar al de juveniles, excepto en la detección de la presa, que fue más simple y rápida en las hembras (Tabla 4). Esta característica puede ser atribuida al aprendizaje y/o motivación alimentaria asociada a la reproducción, mayores en las hembras. Con esta excepción, los resultados obtenidos validan la metodología de Viera (1986) de reunir ambos grupos con fines descriptivos.

En las experiencias 2 y 4 los machos presentaron una fase de detección compleja, con frecuencias altas de toqueteo y tensamiento. Tensamiento se observó con menor frecuencia en juveniles, aunque no se distinguió estadísticamente de los machos de la Experiencia 4. Toqueteo y tensamiento han sido observados por los autores en el cortejo de los machos de esta especie (datos

Tabla 3.—Duraciones medias (\bar{X}) y desviación típica (DT), en segundos, de las fases comportamentales desarrolladas por los cuatro grupos experimentales de *Metepeira* sp. A (N = número de datos).

| Fases | Experiencia 1 | | Experiencia 2 | | Experiencia 3 | | Experiencia 4 | |
|----------------|-------------------|-----|-------------------|-----|--------------------|-----|--------------------|-----|
| | $\bar{X} \pm DT$ | N | $\bar{X} \pm DT$ | N | $\bar{X} \pm DT$ | N | $\bar{X} \pm DT$ | N |
| Detección | 20.4 \pm 16.7 | 19 | 304.3 \pm 412.3 | 17 | 50.4 \pm 59.7 | 23 | 97.5 \pm 110.1 | 19 |
| Inmovilización | 839.9 \pm 614.8 | 19 | 714.8 \pm 482.9 | 12 | 1065.4 \pm 671.0 | 23 | 971.6 \pm 877.5 | 19 |
| Terminal | 75.9 \pm 110.2 | 16 | 72.8 \pm 75.4 | 8 | 207.0 \pm 255.3 | 17 | 86.0 \pm 79.6 | 15 |
| Total | 924.3 \pm 626.1 | 19 | 876.8 \pm 496.7 | 17 | 1268.8 \pm 728.1 | 23 | 1137.0 \pm 896.4 | 19 |

Tabla 4.—Comparación entre las duraciones de las fases comportamentales desarrolladas por los cuatro grupos experimentales, utilizando el test de Student (* = diferencias significativas).

| Fases | Exp. 1-Exp. 2 | Exp. 3-Exp. 4 | Exp. 1-Exp. 3 | Exp. 2-Exp. 4 |
|----------------|---------------|---------------|---------------|---------------|
| Detección | $P = 0.014^*$ | $P = 0.101$ | $P = 0.028^*$ | $P = 0.065$ |
| Inmovilización | $P = 0.562$ | $P = 0.698$ | $P = 0.266$ | $P = 0.304$ |
| Terminal | $P = 0.940$ | $P = 0.075$ | $P = 0.063$ | $P = 0.704$ |
| Total | $P = 0.803$ | $P = 0.611$ | $P = 0.108$ | $P = 0.287$ |

no publicados), lo que sugiere que elementos sexuales se intercalan frecuentemente en el comportamiento alimentario de los machos. Es de destacar que tales elementos también se observaron en machos ubicados en telas de machos juveniles. Esto sugiere una fuerte motivación sexual en los machos adultos, independiente de la presencia o no de estímulos tactoquímicos persistentes (feromona sexual de tela). La presencia de unidades sexuales en la fase inicial de captura contribuiría a la seguridad del macho, inhibiendo posibles ataques pradorios de hembras en condiciones naturales. En los machos, acicalamiento se vinculó predominantemente con desplazamiento (Experiencia 2) o con mordeduras cortas (Experiencia 4): este resultado sugiere que esta unidad pueda cumplir funciones distintas en ambos casos (limpieza de sensores asociados a la detección de la presa y limpieza tegumentaria posterior a las mordeduras, respectivamente). Olivera-Curotti (1984), en *Araneus suspicax* (O.P.-Cambridge) y Viera (1986), en *Meteperia* sp. A, observaron acicalamiento vinculado a la ingestión de la presa. Los machos de la Experiencia 2 presentaron menores frecuencias absolutas de las unidades envolvimiento, mordeduras cortas y transporte, respecto a los machos de la Experiencia 4. Estas diferencias reflejan el hecho de que varios machos de la Experiencia 2 no realizaron fase inmovilización (no atacaron a la presa o no la retuvieron después de demorarse en la detección) y consecuentemente no capturaron la presa. Las dificultades de los machos de la Experiencia 2 para inmovilizar probablemente respondan a una mayor interferencia de elementos sexuales en la fase detección que en los machos de la Experiencia 4, provocada por la feromona sexual persistente en el primer grupo.

Las hembras y los machos de la Experiencia 2 presentaron entre sí diferencias de frecuencias en siete unidades de comportamiento, en la frecuencia de captura de presas y en la duración de la fase detección. Estas diferencias reflejan las características inversas de ambos grupos: como ya fue dicho, las hembras presentaron una detección simple y frecuencias altas de unidades de las fases inmovilización y terminal; los machos, por el contrario, presentaron una detección muy compleja y frecuencias bajas de las unidades de comportamiento en las otras fases.

Los juveniles y los machos de la Experiencia 4 mostraron comportamientos de captura semejantes entre sí, exceptuando la frecuencia de toqueteo y las vinculaciones de acicalamiento; ambas características fueron discutidas más arriba.

En términos generales, los machos desarrollaron una secuencia completa de captura, orientándose inicialmente por las vibraciones de la presa y posteriormente transportando la presa hasta el refugio. Resulta claro que, a diferencia del comportamiento constructor de telas, el comportamiento de captura persiste íntegramente en esta fase particular de la ontogenia. Salvo cinco machos

(Experiencia 2) que persistieron en las fase detección, los machos restantes mostraron completa habilidad de maniobra en un medio que ellos no construyeron. El alejamiento extremo de los machos de la Experiencia 2 en el fenograma de la Fig. 5 destaca la persistencia en la fase detección y también refleja el gran peso que la técnica utilizada otorga a las frecuencias de sucesión más altas (fase inmovilización).

En Araneidae es frecuente que los machos compartan telas con hembras adultas o subadultas, compitiendo entre sí para copular (Robinson y Robinson 1978, 1981; Christenson 1984; Vollrath 1980). Este tipo de competencia parece no existir en *Meteperia* sp. A, que presenta alta densidad poblacional y aparentemente una proporción equivalente de machos y de hembras. Los machos, de tamaño similar a las hembras, no podrían compartir las telas orbiculares con éstas por fuertes interferencias vibratorias y las propias exigencias alimentarias. Los machos de *Meteperia* sp. A mostraron la capacidad de alimentarse sin construir redes de captura ni interferir con las hembras. Esta táctica parece adecuarse a una estrategia de machos poliginos y más o menos longevos. Recientes observaciones de campo indican que los machos podrían reconocer hembras subadultas y permanecer en los hilos periféricos a la tela. Resultan necesarias nuevas observaciones de campo sobre la dinámica de ocupación de telas por machos (¿“robo” de telas, cohabitación con hembras subadultas?), así como nuevos trabajos descriptivos y experimentales a la luz de estas interpretaciones.

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SIX NEW SPECIES OF *DIPLOCENTRUS* PETERS FROM CENTRAL AMERICA (SCORPIONES, DIPLOCENTRIDAE)

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ABSTRACT

Six new species of *Diplocentrus* Peters, 1862 (*D. lucidus* and *D. ornatus* from Belize, *D. coddingtoni*, *D. lourencoi*, and *D. santiagoi* from Honduras, and *D. steeleae* from México) are described. Notes clarifying the composition and distribution of this genus are also given.

INTRODUCTION

The diplocentrid scorpiofauna of Central America (defined as the area of land between the Isthmus of Tehuantepec and the Isthmus of Panamá) is very poorly known. Two genera occur in this region, and are often confused. *Didymocentrus* Kraepelin 1905 is known from six species in the Caribbean (Francke 1978) and three species from El Salvador, southern Honduras, Nicaragua (Kraus 1955; Francke 1978; Lourenço 1983), and Costa Rica (Francke and Stockwell 1987). Four species, *Didymocentrus caboensis* Stahnke, 1968, *Didymocentrus cerralvensis* (Stahnke, 1968), *Didymocentrus comondae* (Stahnke, 1968), and *Didymocentrus cruzensis* (Stahnke, 1968), listed by Stahnke (1968), Williams and Lee (1975), and Williams (1980) from Baja California Sur, México are problematic in their morphological characters and geographic distribution. These species possess a pedipalp chela external carinal structure similar to that of other *Didymocentrus*, in which the external and/or dorsal secondary carina is more prominent than the digital carina (a synapomorphy). They lack the oblique ventromedian keel found on the pedipalp chela and the elongation of the distal lamella found on the hemispermatophores of other *Didymocentrus*. In other respects, e.g., pedipalp chela rugosity, features of the carapace, metasoma, and legs, these species resemble *Didymocentrus*. A detailed study of the morphology and behavior of these species may help to determine their phylogenetic affinities, but for now it seems appropriate to retain them in the genus *Didymocentrus*.

The genus *Diplocentrus* Peters, 1862 is known from Texas, New Mexico, and Arizona in the United States, most of mainland México, Belize, Guatemala, and northern Honduras. Based upon the morphology of the subaculear tubercle (granular), the metasoma (dorsoventrally compressed), and pedipalp chela, two species described from Venezuela, *Diplocentrus flavus* Gonzalez-Sponga, 1983 and *Diplocentrus yustizi* Gonzalez-Sponga, 1983 clearly belong in the genus *Tarsoporosus* Francke, 1978 (= *T. flavus*, and *T. yustizi*, respectively). In addition,

Gonzalez-Sponga (1983) erroneously transferred *Tarsoporosus kugleri* (Schnekenkel, 1932) to *Diplocentrus*. This species should likewise be placed back in the genus *Tarsoporosus*.

The great diversity and local species richness of *Diplocentrus* has been demonstrated by Francke (1977a) for Oaxacan species. Specimens that I have examined indicate that *Diplocentrus* is at least as diverse in Central America. Unfortunately, the secretive habits of the scorpions, the lack of recent collecting efforts, the inaccessibility of some of the collecting areas, and the scarcity of adults among collected specimens has significantly hampered efforts to describe this diversity. A collecting trip to Belize by the author netted but a handful of specimens of *D. maya*, only one of which was a teneral adult male. Without a concerted effort to obtain good series of specimens from Central America, the state of this genus may remain in confusion for some time.

Species of *Diplocentrus* known to occur in Central America (Francke 1977b) include *Diplocentrus anophthalmus* Francke, 1977, *Diplocentrus mitchelli* Francke, 1977, and *Diplocentrus reddelli* Francke, 1977 from México, *Diplocentrus maya* Francke, 1977 from Belize and Guatemala, and *Diplocentrus taibeli* (Caporiacco, 1938) from Guatemala. In this paper, six new species of *Diplocentrus* are described from Belize, Honduras, and México. Although these species are described from one or a few examples, they are distinct enough (as are most species of *Diplocentrus*) to be easily recognized as different species. In fact, twice as many new species were evident to me, but several were represented by juveniles or incomplete specimens, which were unsuitable for use as types. This problem was also encountered by Francke (1977b). Describing these species will increase our knowledge of scorpions in general and might stimulate interest in collecting and studying scorpions from Central America.

METHODS

Measurements and terminology follow Stahnke (1970), except for trichobothriotaxia, which follows Vachon (1974), metasomal and pedipalpal carination, which follows Francke (1978), and hemispermatophore terminology which follows Lamoral (1979). Hemispermatophores were observed in 100% clove oil or lactophenol. All measurements and drawings were made using a dissecting microscope equipped with an ocular micrometer and a drawing tube.

Genus *Diplocentrus* Peters, 1862

Diagnosis.—Pedipalp chela with digital carina always more prominent than dorsal secondary or external secondary carinae; ventral face of chela arched, not flat, with ventromedian carina usually directed distally between the movable finger condyles; surface of chela with reticulate costate pattern, punctation weak to obsolete; base of movable finger of chela opposing fixed finger without a cluster of small tubercles; pedipalp femur width/depth variable. Carapace never noticeably punctate, two or three pairs of lateral eyes present; prolateral pedal spurs present, tarsomere II with or without laterodistal lobes; metasomal segment V with ventral transverse carina; subaculear tubercle not granular. Distal lamella

of hemispermatophore not more than 1.5 times longer than trunk; external lateral margin of median lobe crenulate to strongly denticulate.

Comparisons.—This genus differs from others in the family Diplocentridae (and most Scorpionidae) by the absence of a cluster of small tubercles at the base of the primary row of denticles on the movable finger (an autapomorphy). It differs from *Heteronebo* Pocock, 1899 and *Nebo* Simon, 1878 by the presence of a ventral transverse carina on metasomal segment V. *Diplocentrus* differs from *Cazierius* Francke, 1978, *Oiclus* Simon, 1880, and *Tarsoporosus* Francke, 1978 by having the ventral face of the pedipalp chela arched rather than flat. *Didymocentrus* differs from *Diplocentrus* by having the external secondary or dorsal secondary carinae of the pedipalp chela more prominent than the digital carina and by lacking a reticulate costate pattern on the pedipalps. Most *Didymocentrus* (except Baja California species) also have the ventromedian carina of the pedipalp chela directed toward the internal movable finger condyle, and have the distal lamella of the hemispermatophore more than twice the length of the trunk. *Diplocentrus tehuano* Francke, 1977 and *D. ornatus*, however, exhibit a distinctly oblique ventromedian carina like that found in *Didymocentrus*.

Diplocentrus lucidus, new species

Figs. 1-6

Type data.—Holotype female with 28 first instar young (paratypes) from Blue Hole, Cayo District, Belize, 22 August 1982 (no collector), deposited in the University of Georgia Museum of Natural History, Athens, Georgia.

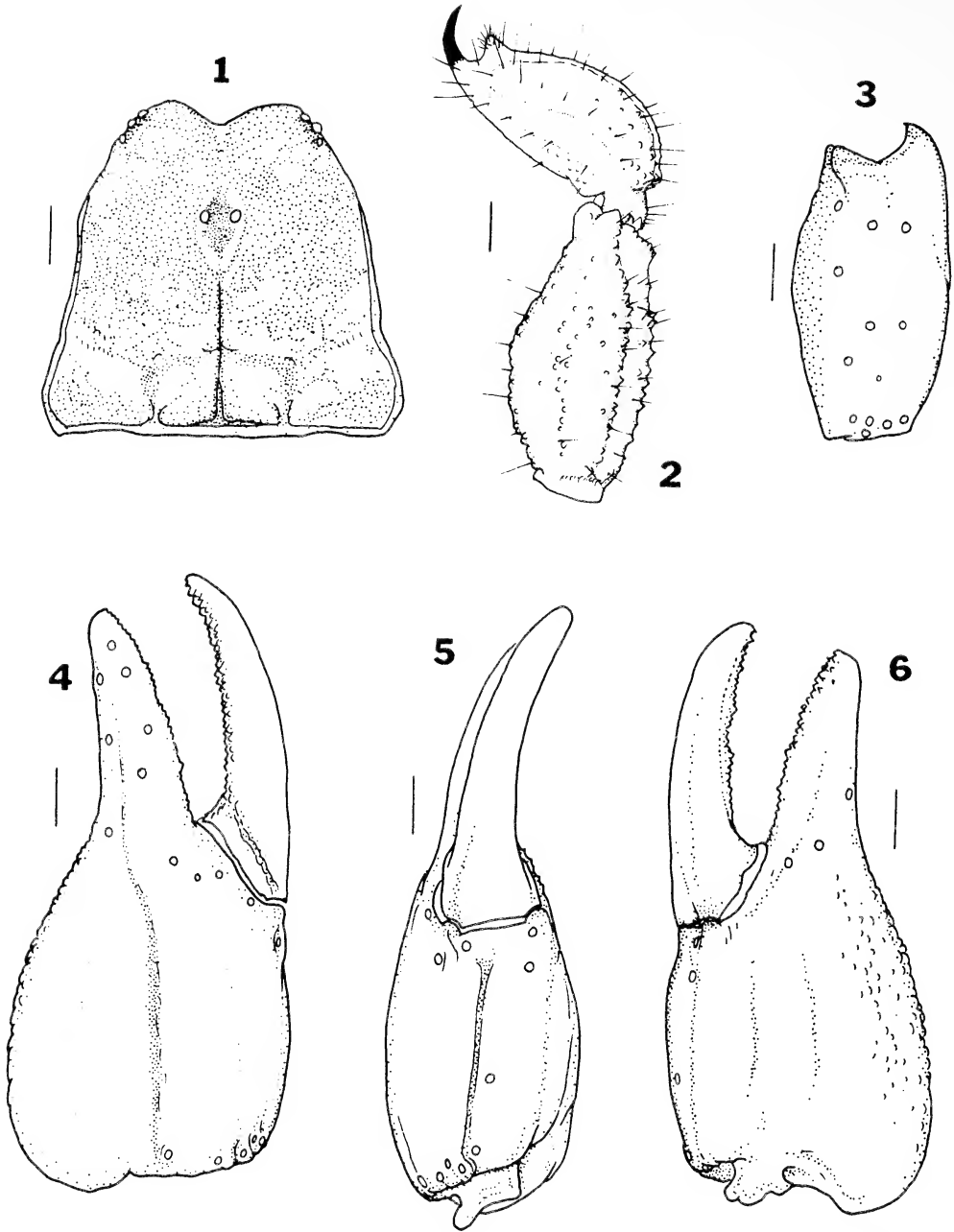
Etymology.—The specific epithet is from the Latin *lucid* and refers to the shiny appearance of this holotype.

Distribution.—Known only from the type locality.

Diagnosis.—Dark scorpion; adult female 42 mm long; carapace sparsely granular, wider than long; pectinal tooth count 11-13; genital operculi with three pairs of setae; tarsomere II spine formula 4-5/5:5-6/5-6:7/7:7/7; pedipalp chela of female smooth; pedipalp chela length/depth 2.06; pedipalp chela width/depth 0.69.

Description.—*Female*: Brown with variable dark brown marbling. Carapace minutely granular along margins, wider than long (Fig. 1); prosomal venter smooth, lustrous, sparsely punctate; pectinal tooth count 11-12. Genital operculi bearing three pairs of setae. Mesosomal tergites smooth, moderately punctate; weakly granular along the posterior margin; tergite VII granular posterolaterally, not bilobate; submedian and lateral carinae obsolete, indicated by a few large granules. Mesosomal sternites smooth, moderately punctate; sternite VII with submedian carinae vestigial, smooth; lateral carinae weak, smooth.

Metasoma intercarinal spaces granular. Dorsolateral and lateral supramedian carinae moderately strong, granulose on all segments. Lateral inframedian carinae complete on all segments; weak, granulose. Ventrolateral carinae moderate; finely granulose on segment I; smooth on II; subgranulose on III; granulose on IV. Ventral submedian carinae weak, smooth on segments I and II; obsolete, granular on III and IV. Metasomal segment V (Fig. 2) with dorsolateral carinae strong, granular; lateromedian carinae present on anterior one-half, weak, granular;



Figs. 1-6.—*Diplocentrus lucidus*, new species, holotype female: 1, carapace; 2, metasomal segment V and telson, lateral aspect; 3-6, pedipalp; 3, patella, external aspect; 4, chela, external aspect; 5, chela, ventral aspect; 6, chela, internal aspect. Scale bars = 1 mm.

ventrolateral and ventromedian carinae strong, tuberculate; ventral transverse carina weak, tuberculate; anal subterminal carina strong, crenulate; terminal carina obsolete. Telson (Fig. 2) smooth with a row of tubercles on the ventral anterior surface; moderately setose.

Pedipalps with orthobothriotaxy C (Vachon 1973). Femur with dorsal and internal faces granular; other faces smooth; dorsointernal carina weak to

moderate, granulose; dorsoexternal carina moderate, granulose; ventroexternal carina obsolete; ventrointernal carina weak to moderate, granulose. Patella (Fig. 3) with ventral and external faces smooth; internal face minutely granular; basal tubercle weak, granulose; dorsomedian carina moderately strong, smooth; ventroexternal carina weak, smooth; ventrointernal carina moderate, granulose; other carinae obsolete. Chela (Figs. 4-6) with external, ventral, and internal faces smooth; dorsal marginal carina vestigial, granular; digital carina weak to moderate, smooth; ventromedian carina moderately strong, smooth; ventrointernal carina weak, smooth; all internal carinae weak, smooth to weakly granular. All other carinae vestigial to obsolete, smooth.

Legs with tarsomeres weakly granular, other segments smooth. Tarsomere II spine formula 4-5/5:5-6/5-6:7/7:7/7.

Morphometrics.—Carapace wider than long; metasomal segments I and II wider than long. Pedipalp chela length/depth 2.06; pedipalp chela width/depth 0.69; pedipalp chela length/pedipalp fixed finger length 2.51; pedipalp chela length/carapace length 1.65; carapace length/pedipalp fixed finger length 1.53; pedipalp fixed finger length/pedipalp femur length 0.87; pedipalp fixed finger length/metasomal segment V length 0.76.

Variation.—Pectinal teeth were counted on 28 first instar young captured with the holotype. Although they cannot be reliably sexed before the third instar, both males and females are likely to be represented in this litter. Specimens varied in pectinal tooth counts as follows: 23 combs with 11 teeth; 31 combs with 12 teeth; 4 combs with 13 teeth. Other taxonomically important structures were not sufficiently developed to be of use in this description.

Comparisons.—This species may be distinguished from *D. taibeli*, *D. mitchelli*, *D. lourencoi*, and *D. santiagoi* by its smaller size and lower number of setae on the genital operculi (three pairs versus six to ten pairs). It may be distinguished from the remaining Central American *Diplocentrus* by having the carapace wider than long (all others with carapace longer than wide) and by its high tarsomere II spine formula.

Specimens examined.—Known only from the holotype and its young.

Diplocentrus ornatus, new species

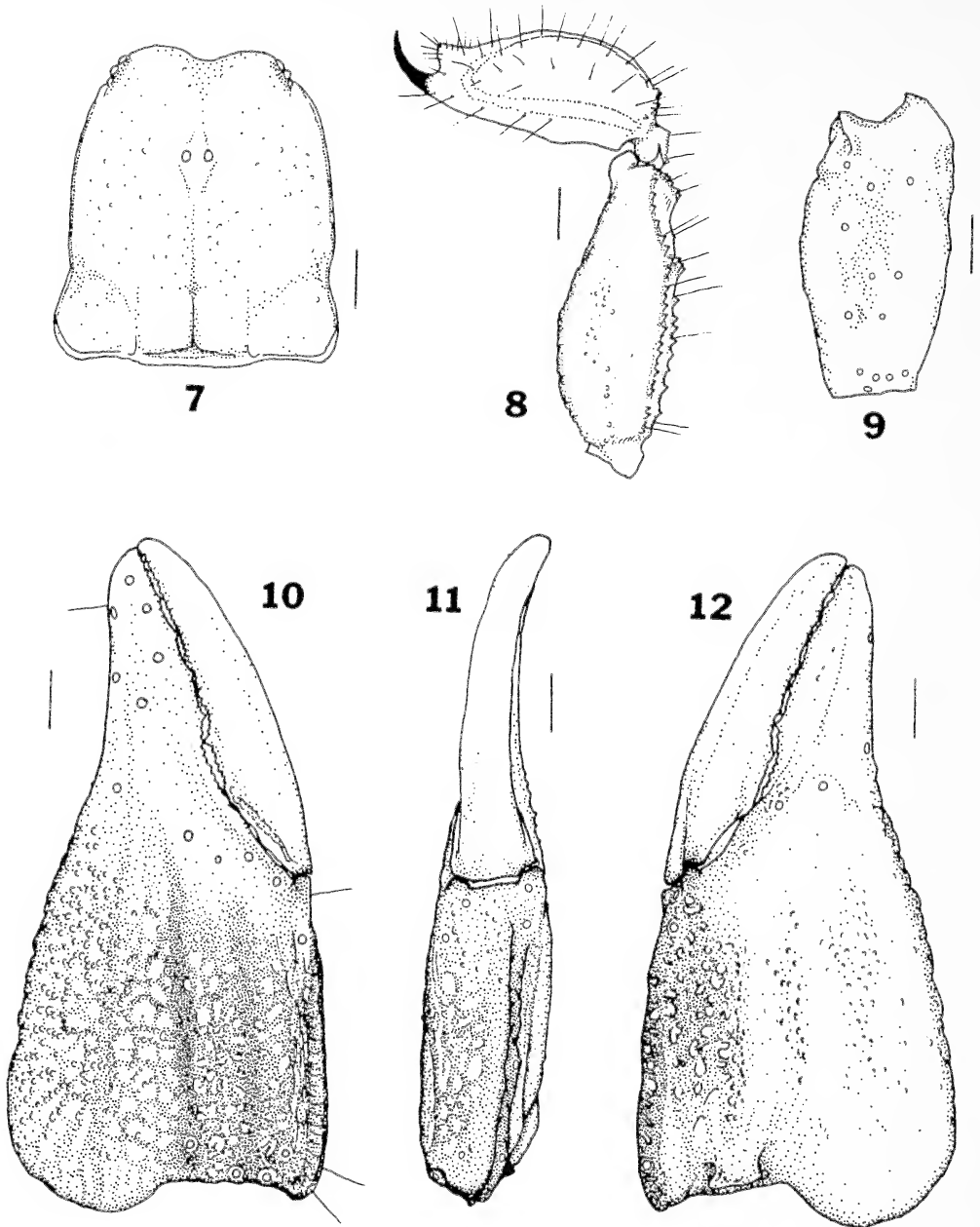
Figs. 7-18

Type data.—Holotype male and two female paratypes from Bokowina, Stann Creek District, Belize, 21 October 1939 (I. T. Sanderson), deposited in the Field Museum of Natural History, Chicago.

Etymology.—The specific epithet is from the Latin *ornat* and refers to the delicately sculptured pedipalps of the male of this species.

Distribution.—Known only from the type locality.

Diagnosis.—Reddish scorpions; adults 30 to 38 mm long; carapace moderately granular, much longer than wide; pectinal tooth counts 10-11 in males, 10 in females; genital operculi with two or three pairs of setae; modal tarsomere II spine formula 4/4:5/5:6/6:6/6; males with weak to moderate reticulate costate pattern on pedipalp, female pedipalp with vestigial reticulation; pedipalp chela length/depth 2.16 in male, 2.13-2.15 in females; pedipalp chela width/depth 0.43 in male, 0.59-0.60 in females.



Figs. 7-12.—*Diplocentrus ornatus*, new species, holotype male: 7, carapace; 8, metasomal segment V and telson, lateral aspect; 9-12, pedipalp; 9, patella, external aspect; 10, chela, external aspect; 11, chela, ventral aspect; 12, chela, internal aspect. Scale bars = 1 mm.

Description.—*Male*: Color light reddish brown without dark brown marbling. Carapace moderately granular, much longer than wide (Fig. 7); prosomal venter smooth, weakly punctate; pectinal tooth count 10-11. Genital operculi bearing two or three pairs of setae. Mesosomal tergites densely granular; tergite VII moderately bilobate, coarsely granular; submedian and lateral carinae obsolete. Mesosomal sternites coriaceous, weakly punctate; sternite VII with submedian carinae obsolete; lateral carinae vestigial, subgranulose.

Metasoma intercarinal spaces weakly granular. Dorsolateral carinae weak, sparsely granulose on segments I-IV. Lateral supramedian carinae weak, granulose on segments I-IV. Lateral inframedian carinae interrupted, vestigial to obsolete, weakly granulose on segments I-IV. Ventrolateral carinae weak, smooth on segments I-III; moderate, weakly granulose on IV. Ventral submedian carinae weak to vestigial, smooth on segments I and II; obsolete on III and IV. Metasomal segment V (Fig. 8) dorsolateral carinae weak to moderate, granulose; lateromedian carinae obsolete, represented by a line of small, scattered granules; ventrolateral carinae moderate, sharply granulose; ventromedian carina weak to moderate, sparsely granular; ventral transverse carina moderate, tuberculate; anal subterminal carina moderate, sparsely crenulate; anal terminal carina obsolete. Telson (Fig. 8) smooth, weakly granulose along anteroventral face; moderately setose.

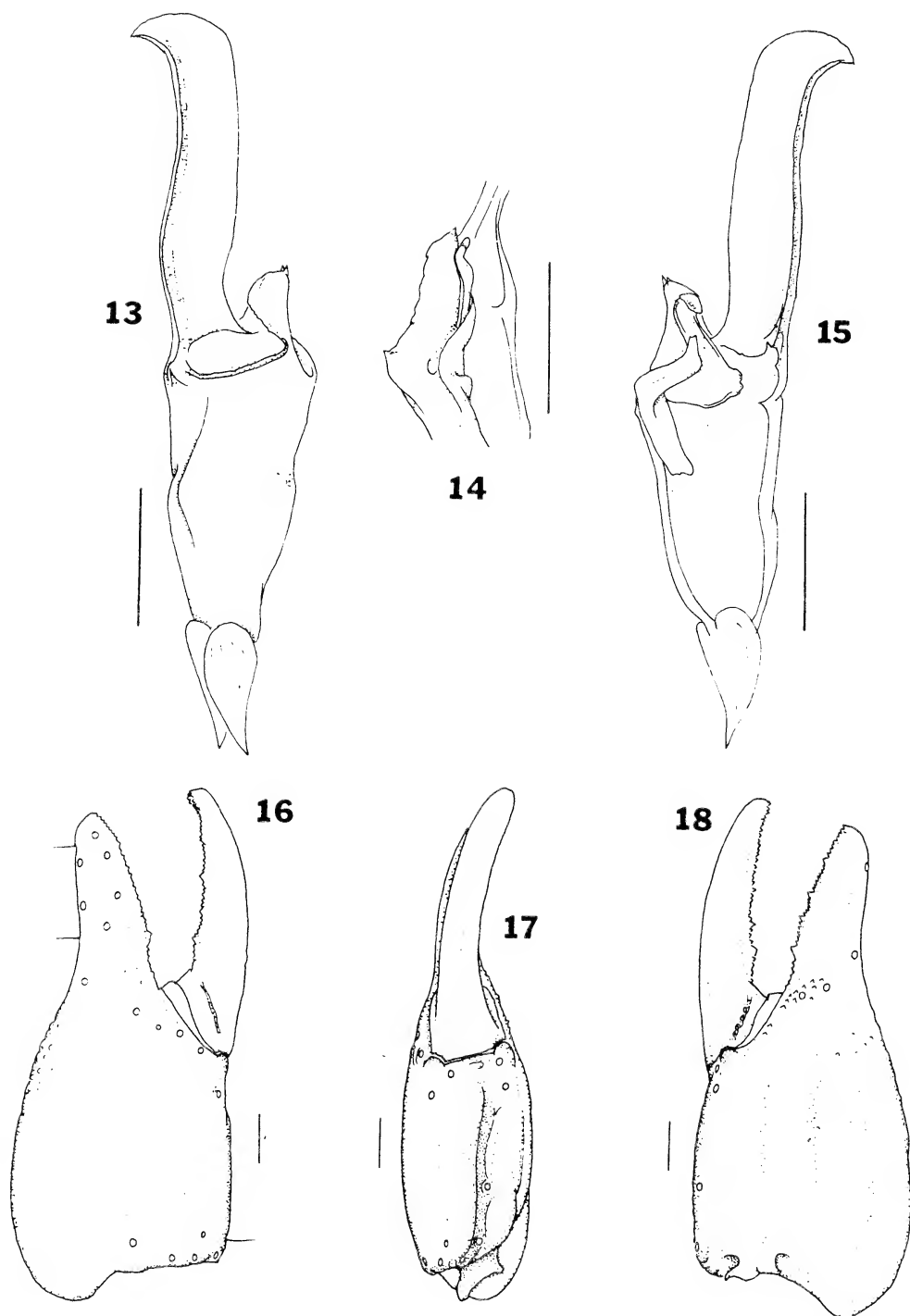
Pedipalps with orthobothriotaxy C (Vachon 1973). Femur with dorsal and internal faces very sparsely granular, interspersed with small tubercles; ventral and external faces sparsely, minutely granular; dorsointernal, dorsoexternal, and ventrointernal carinae weak, variably tuberculate; ventroexternal carina obsolete. Patella (Fig. 9) with ventral and external faces smooth; internal face granular; basal tubercle moderate with one or two hook-like denticles; dorsomedian carina moderate, smooth; ventroexternal carina weak to vestigial, smooth; ventrointernal carina weak, granulose; other carinae obsolete. Chela laterally compressed (Figs. 10-12) with dorsal, ventral, and external faces weakly to moderately reticulate; internal face vestigially reticulate; dorsal marginal carina moderate, granulose; dorsal secondary carina vestigial, smooth; digital carina moderate, smooth; external secondary carina vestigial, reticulate; ventroexternal carina weak, reticulate; ventromedian carina very strong, directed distally toward internal movable finger condyle, produced into a flange extending proximally along basal margin of chela to digital carina; ventrointernal carina obsolete; internal carinae vestigial to obsolete.

Legs sparsely granular. Tarsomere II spine formula 4/4:5/5:6/6:6/6.

Hemispermaphore (Figs. 13-15) lamelliform; lateral external margin of median lobe armed with several low, rounded denticles; inner lobe bearing a distal projection along the ventral margin.

Females differ from male as follows. Carapace and mesosomal tergites weakly, sparsely granular; pedipalps and metasoma less granular. Pedipalp chela (Figs. 16-18) with all faces vestigially reticulate to smooth, dorsal face granular; dorsal marginal, dorsal secondary, digital, secondary dorsal, and internal carinae vestigial; ventromedian carina moderate to strong; all other carinae obsolete. Pectinal tooth count 10.

Morphometrics.—Carapace longer than wide; pedipalps elongate, those of male larger than those of female; all metasomal segments longer than wide in male; metasomal segment I wider than long in females. Pedipalp chela length/depth 2.16 in male, 2.13-2.15 in females; pedipalp chela width/depth 0.43 in male, 0.59-0.60 in females; pedipalp chela length/pedipalp fixed finger length 2.49 in male, 2.46-2.52 in females; pedipalp chela length/carapace length 1.94 in male, 1.72-1.74 in females; carapace length/pedipalp fixed finger length 1.28 in male, 1.44-1.45 in females; pedipalp fixed finger length/pedipalp femur length 0.98 in male, 0.93 in females; pedipalp fixed finger length/metasomal segment V length 0.80 in male, 0.81-0.82 in females.



Figs. 13-18.—*Diplocentrus ornatus*, new species: 13-15, right hemispermatophore of holotype male; 13, dorsal aspect; 14, detail of capsular region, ectal aspect; 15, ventral aspect; 16-18, right pedipalp chela of female; 16, external aspect; 17, ventral aspect; 18, internal aspect. Scale bars = 1 mm.

Variation.—Specimens varied in pectinal tooth counts as follows: male, one comb with ten teeth, one comb with 11 teeth; females, four combs with ten teeth. Tarsomere II spine counts differed from the typical formula as follows: two leg I's with 4/5; one leg II with 4/5; one leg III with 5/6; one leg III with 6/7; one leg IV with 6/7.

Habitat.—The three type specimens were collected "in a hole in moist loam."

Comparisons.—*Diplocentrus ornatus* can be distinguished from *D. taibeli*, *D. mitchelli*, *D. lourencoi*, and *D. santiagoi* by its smaller size and lower number of setae on the genital operculi (two to three pairs versus six to ten pairs). This species differs from *D. lucidus*, *D. reddelli*, *D. maya*, *D. anophthalmus*, and *D. coddingtoni* by its lower pedipalp chela width/depth (less than or equal to 0.60 versus greater than 0.60), the absence of dusky marbling on the carapace, and the position of the ventromedian carina of the pedipalp chela (directed toward the movable finger inner condyle rather than medially between the inner and outer condyle). *Diplocentrus ornatus* differs from its close relative *D. steeleae*, by its larger size, its greater pedipalp chela length/depth (greater than 2.00 versus less than 2.00), and its hemispermatophore (lateral external margin of median lobe weakly dentate in *D. ornatus*, strongly dentate in *D. steeleae*).

Specimens examined.—Known only from the holotype and two paratypes.

***Diplocentrus lourencoi*, new species**

Figs. 19-24

Type data.—Holotype female from Río Santa Ana Canyon (3500 ft.), San Pedro Sula, Departamento Cortés, Honduras, 21 March 1923 (K. Schmidt and L. Walters), Capt. Field Mus. Exped., deposited in the Field Museum of Natural History, Chicago.

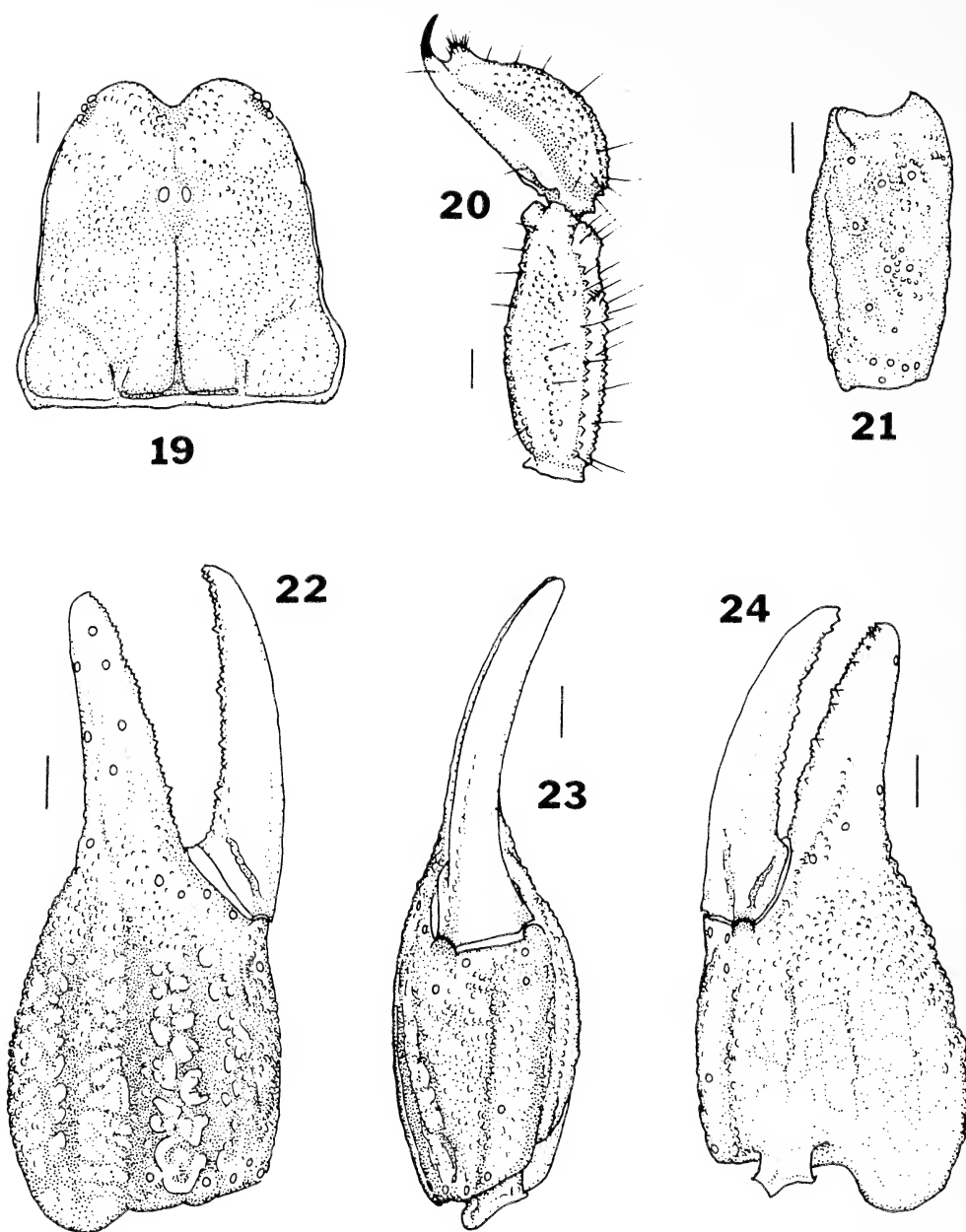
Etymology.—The specific epithet honors fellow scorpionologist Dr. Wilson R. Lourenço, in recognition of his contributions to scorpion systematics, biogeography, and biology.

Distribution.—Known only from the type locality.

Diagnosis.—Dark scorpion; 50 mm in total length; carapace densely, coarsely granular, wider than long; pectinal tooth count 9-10 in females, males unknown; genital operculi with eight to ten pairs of setae; modal tarsomere II spine formula 4/5:5/5:5/6:5/6; female pedipalp with weak reticulation; pedipalp somewhat elongate; pedipalp chela length/depth 2.29; pedipalp chela width/depth 0.66.

Description.—*Female*: Color brown with variable dark brown marbling. Carapace densely, coarsely granular, posterior width greater than length (Fig. 19); prosomal venter coriaceous, punctate; pectinal tooth count 9-10. Genital operculi bearing eight to ten pairs of setae. Mesosomal tergites minutely granular; tergite VII not bilobate, acarinate. Mesosomal sternites smooth to coriaceous, punctate; sternite VII submedian carinae vestigial, smooth; lateral carinae weak, smooth.

Metasoma intercarinal spaces coarsely granular. Dorsolateral carinae moderate, granular on segments I-IV. Lateral supramedian carinae moderate, granular on segments I-IV. Lateral inframedian carinae granular; weak, complete on segments I-III; vestigial, incomplete on IV. Ventrolateral carinae moderate, granulose on segments I-IV. Ventral submedian carinae granular; weak on segments I and II; vestigial on III; obsolete on IV. Metasomal segment V (Fig. 20) dorsolateral



Figs. 19-24.—*Diplocentrus lourencoi*, new species, holotype female: 19, carapace; 20, metasomal segment V and telson, lateral aspect; 21-24, pedipalp; 21, patella, external aspect; 22, chela, external aspect; 23, chela, ventral aspect; 24, chela, internal aspect. Scale bars = 1 mm.

carinae moderate, granular; lateromedian carinae weak, granular on anterior one-half; ventrolateral, ventromedian and ventral transverse carinae moderate to strong, tuberculate; anal subterminal carina moderate, subtuberculate; anal terminal carina weak, granulose. Telson (Fig. 20) moderately granular; sparsely hirsute.

Pedipalps with orthobothriotaxy C (Vachon 1973). Femur with dorsal and internal faces coarsely granular; ventral and external faces minutely granular;

dorsointernal and dorsoexternal carinae moderate, granular; ventrointernal carina vestigial, granular; other carinae obsolete. Patella (Fig. 21) with ventral and external faces weakly reticulate, granular; internal face coarsely granular; basal tubercle strong, granular; dorsomedian carina strong, granular; dorsoexternal carina weak, granular; ventroexternal carina weak to moderate, granular; ventrointernal carina weak, granular; other carinae obsolete. Chela (Figs. 22-24) with all faces weakly reticulate, these reticulae granular; dorsal, internal, and ventral faces, and external face at base of fixed finger granular; dorsal marginal carina vestigial, granular; dorsal secondary carina weak to vestigial, granular; digital carina weak to moderate, smooth; external secondary carinae weak to vestigial, granular; ventroexternal carina obsolete; ventromedian carina strong, granular; ventrointernal carina weak, granular; internal carinae weak, granular.

Legs minutely granular. Tarsomere II spine formula 4/5:5/5:5/6:5/6.

Morphometrics.—All metasomal segments longer than wide; carapace wider than long. Pedipalp chela length/depth 2.29; pedipalp chela width/depth 0.66; pedipalp chela length/pedipalp fixed finger length 2.27; pedipalp chela length/carapace length 1.87; carapace length/pedipalp fixed finger length 1.21; pedipalp fixed finger length/pedipalp femur length 0.98; pedipalp fixed finger length/metasomal segment V length 0.89.

Comparisons.—This species is distinguished from *D. reddelli*, *D. maya*, *D. anophthalmus*, *D. coddingtoni*, *D. lucidus*, *D. ornatus*, and *D. steeleae* by its larger size and greater number of setae on the genital operculi (eight to ten pairs versus two to four pairs). It can be separated from *D. taibeli* and *D. mitchelli* by its lower pectinal tooth counts (nine to ten versus 15-17) and the presence of weak reticulation on all pedipalp chela faces (lacking in *D. taibeli* and *D. mitchelli*). *Diplocentrus lourencoi* differs from *D. santiagoi* by its slightly lower pectinal tooth count (nine to ten versus 12), its slightly higher number of setae on the genital operculi (eight to ten pairs versus seven pairs), and the granulation of the carapace and telson (densely, coarsely granular in *D. lourencoi*, smooth to weakly granular in *D. santiagoi*).

Specimens examined.—Known only from the holotype.

Diplocentrus coddingtoni, new species

Figs. 25-36

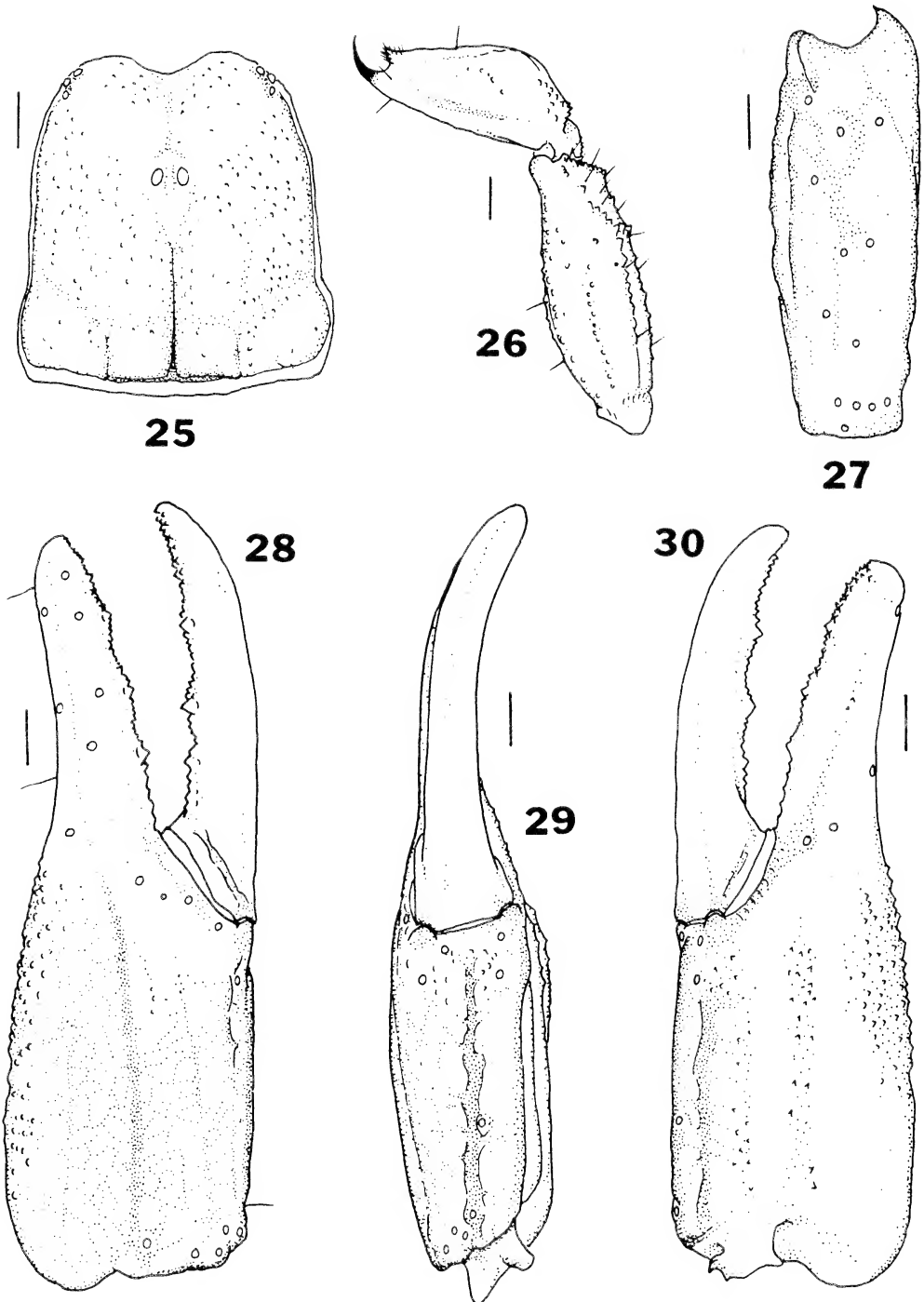
Type data.—Holotype male and paratypes from La Ceiba, Departamento Atlántida, Honduras, 1920 (W. L. Mann), deposited in the U.S. National Museum, Washington, D.C. USA.

The types were found in separate vials, some labelled "*Didymocentrus ceibaensis* Stahnke, M.S. name?, 1984?" and the others labelled "*Didymocentrus hondurensis* Stahnke, M.S. name?, 1984?" apparently by museum staff. These names were never published and are not valid. In addition, the specimens were identified to the wrong genus, and the sexes were thought to be different species.

Etymology.—Named in honor of Dr. Jonathan Coddington, Curator of Arachnida and Myriapoda, U.S. National Museum.

Distribution.—Known only from the type locality.

Diagnosis.—Dark scorpions; adults 35 to 45 mm long; carapace coarsely, minutely granular, much longer than wide; pectinal tooth counts 11 in males, 10-



Figs. 25-30.—*Diplocentrus coddingtoni*, new species, holotype male: 25, carapace; 26, metasomal segment V and telson, lateral aspect; 27-30, pedipalp; 27, patella, external aspect; 28, chela, external aspect; 29, chela, ventral aspect; 30, chela, internal aspect. Scale bars = 1 mm.

11 in females; genital operculi with two or three pairs of setae; modal tarsomere II spine formula 4/4:4/5:5/5:5/5. Males with weak reticulate costate pattern on pedipalp; female pedipalp with vestigial reticulation. Strongly sexually dimorphic; pedipalp chela length/depth 2.98 in male, 2.07-2.22 in female; pedipalp chela width/depth 0.63 in male, 0.58-0.64 in female.

Description.—*Male*: Color brown with variable dark brown marbling. Carapace coarsely, minutely granular, much longer than wide (Fig. 25); prosomal venter coriaceous to vestigially granular, very sparsely punctate; pectinal tooth count 11-11. Genital operculi bearing two to three pairs of setae. Mesosomal pretergites coriaceous; tergites shagreened, interspersed with weak granulation; tergite VII acarinate; moderately bilobed, coarsely granular posterolaterally. Mesosomal sternites sparsely, minutely granular, finely punctate; sternite VII with submedian and lateral carinae weak to vestigial, smooth.

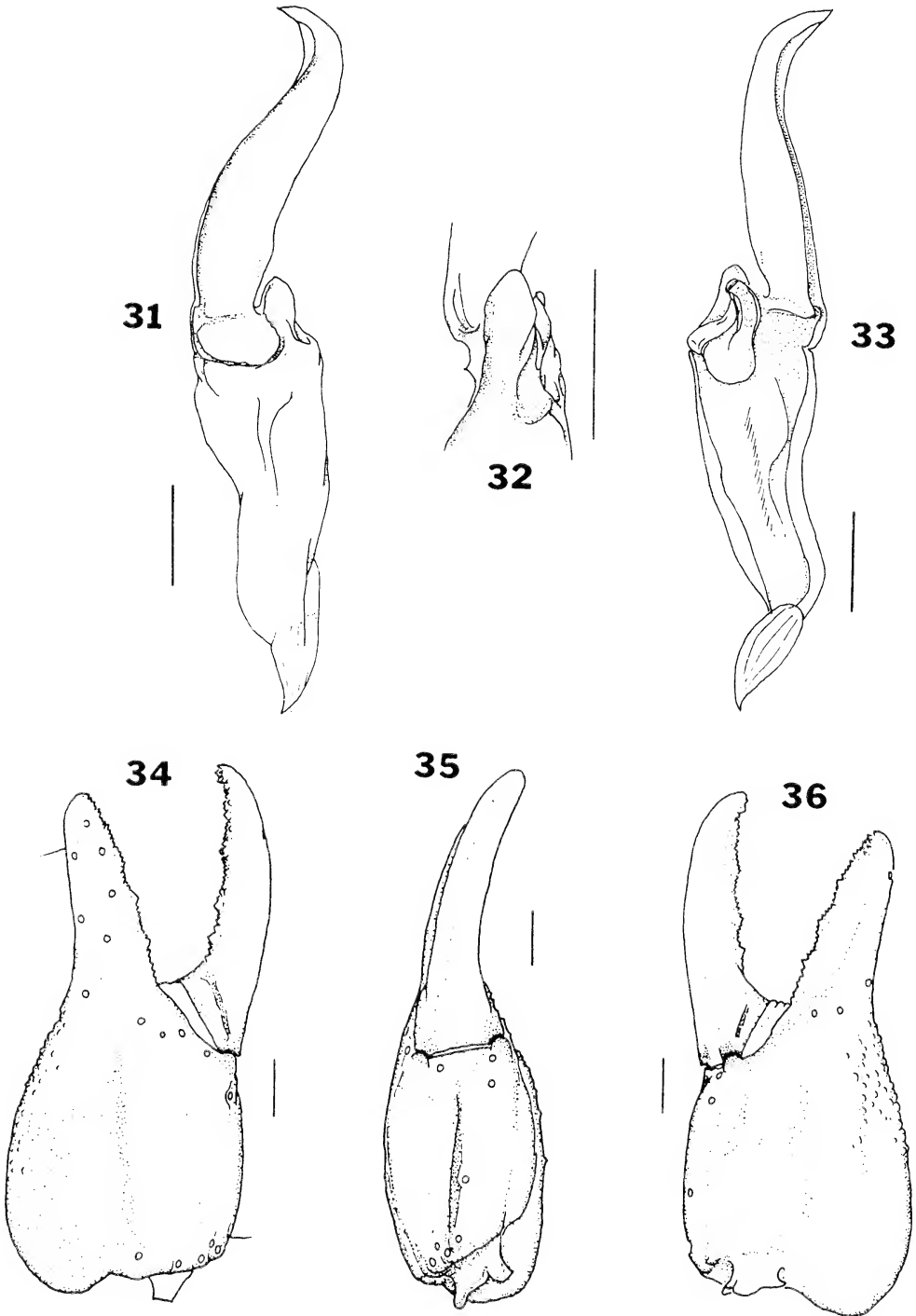
Metasoma intercarinal spaces coarsely, minutely granular dorsally, smooth ventrally. Dorsolateral carinae weak, on segment I; moderate on II, III; and strong on IV; tuberculate. Lateral supramedian carinae moderate on segment I; strong on II-IV; sharply tuberculate. Lateral inframedian carinae moderate on segments I-III; weak on IV; serrate to subserrate. Ventrolateral carinae moderate, smooth on segments I-IV. Ventral submedian carinae smooth, weak to moderate on segments I and II; weak on III; vestigial on IV. Metasomal segment V (Fig. 26) minutely granular on lateral, anterior dorsal, and anterior ventral faces; lateromedian areas of dorsal surface with numerous sharp granules; dorsolateral carinae moderate, irregularly granulose; lateromedian carinae vestigial, irregularly granular; ventrolateral, ventromedian and ventral transverse carinae moderate to strong each with a single row of sharp tubercles; anal subterminal carina moderate, granulose; anal terminal carina obsolete. Telson (Fig. 26) smooth, with a few tubercles on the anterior ventral surface, sparsely setose.

Pedipalps with orthobothriotaxy C (Vachon 1973). Femur with internal face moderately tuberculate; other faces minutely granular; dorsointernal carina weak to moderate with well separated large tubercles; dorsoexternal carina weak to vestigial distally, granulose; ventroexternal carina obsolete; ventrointernal carina weak to obsolete distally, tuberculate. Patella (Fig. 27) with ventral and external faces vestigially reticulate; internal face coarsely granular; basal tubercle moderately strong, bifurcate; dorsomedian carina moderate, smooth; ventroexternal carina weak to vestigial; ventrointernal carina weak, sparsely granulose; other carinae obsolete. Chela (Figs. 28-30) with dorsal face weakly reticulate; other faces lacking reticulate costate pattern; dorsal marginal carina moderate to strong, granulose; dorsal secondary carina weak, weakly reticulate; digital carina strong, smooth; external secondary carina vestigial, weakly reticulate; ventroexternal carina obsolete; ventromedian carina moderate to strong, reticulate; ventrointernal carina weak to moderate, smooth; internal carinae weak, smooth ventrally, granular dorsally. Fingers of chela noticeably thick, without taper.

Legs lustrous, carinae granular. Tarsomere II spine formula 4/4:4/5:5/5:5/5.

Hemispermaphore (Figs. 31-33) lamelliform; lateral margin of capsular lobe armed with a few weak denticles; inner lobe bearing a projection distally.

Females differ from male as follows. Carapace and tergites weakly granular; venter and sternites smooth, lustrous; sternite VII with submedian carinae vestigial. Metasomal intercarinal spaces smooth; dorsolateral carinae weak to moderate, granulose; lateral supramedian carinae weak to moderate, granulose;



Figs. 31-36.—*Diplocentrus coddingtoni*, new species: 31-33, right hemispermatophore of holotype male; 31, dorsal aspect; 32, detail of capsular region, ectal aspect; 33, ventral aspect. 34-36, pedipalp chela of paratype female; 34, external aspect; 35, ventral aspect; 36, internal aspect. Scale bars = 1 mm.

lateral inframedian carinae weak to vestigial; ventrolateral carinae moderate to weak, weakly granulose to smooth; ventral submedian carinae weak, granulose on segments I and II, vestigial, smooth on III, obsolete on IV. Metasomal segment V less granular; dorsolateral carinae weak, subgranulose. Telson not elongate, vestigially granular. Pedipalp less granular, not elongate; chela (Figs. 34-36) vestigially reticulate dorsally; all carinae weaker, smooth; pectinal tooth count 10-11.

Morphometrics.—Sexes are strongly dimorphic in some characters. Carapace longer than broad; pedipalp greatly elongate in males; all metasomal segments longer than wide on male; metasomal segments I and II as wide as or wider than long on female. Pedipalp chela length/depth 2.98 in male, 2.07-2.22 in females; pedipalp chela width/depth 0.63 in male, 0.58-0.64 in females; pedipalp chela length/pedipalp fixed finger length 2.44 in male, 2.35-2.45 in females; pedipalp chela length/carapace length 2.08 in male, 1.66-1.78 in females; carapace length/pedipalp fixed finger length 1.17 in male, 1.32-1.45 in females; pedipalp fixed finger length/pedipalp femur length 0.78 in male, 0.89-0.98 in females; pedipalp fixed finger length/metasomal segment V length 0.87 in male, 0.84-0.89 in females.

Variation.—Paratype tarsomere II spine counts 4/4, X/X on leg II; 5/X, X/X on leg IV. Pectinal tooth counts on females varied as follows: six combs with 10 teeth, two combs with 11 teeth.

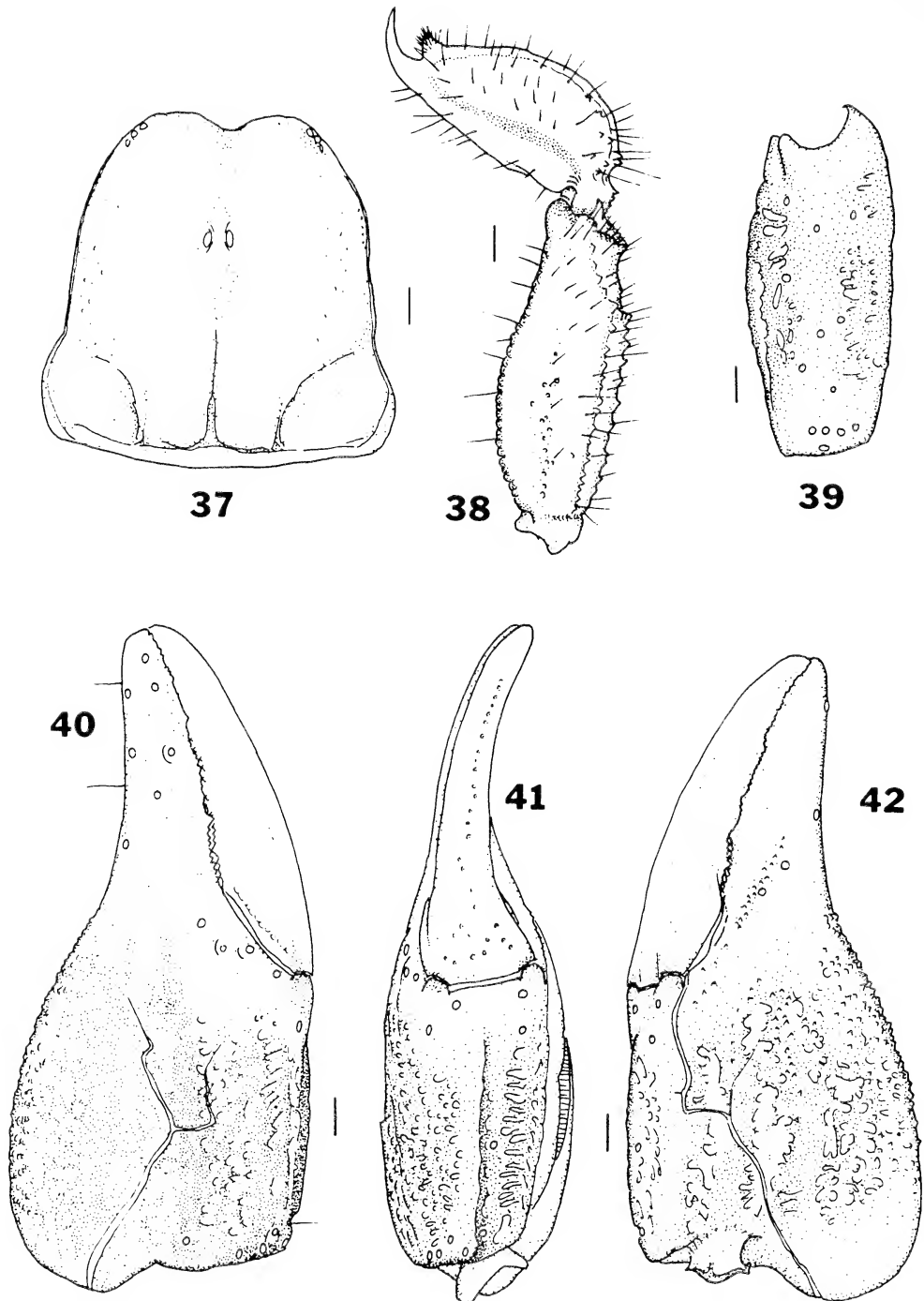
Comparisons.—This species can be distinguished from *D. taibeli*, *D. mitchelli*, *D. lourencoi*, and *D. santiagoi* by its lower number of setae on the genital operculi (two to three pairs versus six to ten pairs). *Diplocentrus coddingtoni* can be distinguished from *D. lucidus* by its narrower carapace and lower tarsomere II spine formula (4/4:4/5:5/5:5/5 versus 4-5/5:5-6/5-6:7/7:7/7). It differs from *D. ornatus* and *D. steeleae* by its greater male pedipalp chela length/depth (2.98 versus 1.93 and 2.16), male pedipalp chela width/depth (0.64 versus 0.43-0.48), and in the placement of the distal projection of the inner lobe of the hemispermatophore (along the dorsal margin in *D. coddingtoni*, along the ventral margin in *D. ornatus* and *D. steeleae*). *Diplocentrus coddingtoni* differs from *D. reddelli* and *D. maya* by its pedipalp chela length/depth (2.98 and 2.07 for male and female of *D. coddingtoni*, 2.40-2.50 and 2.27-2.42 for males and females of *D. maya*, 2.56 for male of *D. reddelli*) and the degree of granulation on the carapace (minute, coarse granulation on *D. coddingtoni* male, sparsely granulose on *D. maya* male, shagreened on *D. reddelli* male). *Diplocentrus anophthalmus* is troglobitic and differs from *D. coddingtoni* by its lack of median eyes, pigmentation, and pedipalp chelal carinae.

Specimens examined.—In addition to the holotype, four female and two juvenile male paratopotypes.

Diplocentrus santiagoi, new species

Figs. 37-42

Type data.—Holotype female from Copán, Departamento Copán, Honduras, 4 March 1939 (no collector), deposited in the American Museum of Natural History, New York.



Figs. 37-42.—*Diplocentrus santiagoi*, new species, holotype female: 37, carapace; 38, metasomal segment V and telson, lateral aspect; 39-42, pedipalp; 39, patella, external aspect; 40, chela, external aspect (note fracture); 41, chela, ventral aspect; 42, chela, internal aspect. Scale bars = 1 mm.

Etymology.—Named for my good friend and fellow scorpialogist, Jorge A. Santiago-Blay, in recognition of his contributions to scorpion taxonomy.

Distribution.—Known only from the type locality.

Diagnosis.—Dark brown scorpions; adults 60 mm long; carapace weakly granular, wider than long; genital operculi with seven pairs of setae; pectinal tooth count 12 in female, males unknown; modal tarsomere II spine formula 5/5:5/5:6/6:6/6; pedipalp of female somewhat elongate, weakly reticulate on all faces; pedipalp chela length/depth 2.17; pedipalp chela width/depth 0.63.

Description.—*Female*: Brown with variable dark brown marbling. Carapace weakly granular along the anterior and lateral margins, and along the median furrow; wider than long (Fig. 37); prosomal venter smooth, punctate; pectinal tooth count 12-12. Genital operculi bearing seven pairs of setae. Mesosomal tergites smooth; tergite VII granular; not bilobate; submedian and lateral carinae obsolete, represented by a few large granules. Mesosomal sternites smooth, densely punctate; sternite VII with submedian and lateral carinae very weak to vestigial, smooth.

Metasoma intercarinal spaces minutely granular. Dorsolateral carinae moderate, granulose on segments I-IV. Lateral supramedian carinae moderate, granulose on segments I-IV. Lateral inframedian carinae granulose; complete, moderate on segment I, weak on II and III; incomplete, vestigial on IV. Ventrolateral carinae moderate, granulose on segments I-III; weak, crenate on IV. Ventral submedian carinae weak, subgranulose on segments I and II; vestigial, smooth on III; vestigial to obsolete, smooth on IV. Metasomal segment V (Fig. 38) dorsolateral carinae moderate, granulose; lateromedian carinae very weak, granular on anterior one-half; ventrolateral, ventromedian and ventral transverse carinae moderate to strong, tuberculate; anal subterminal carina strong, crenulate; anal terminal carina obsolete. Telson (Fig. 38) sparsely tuberculate anteroventrally, otherwise smooth.

Pedipalp with orthobothriotaxy C (Vachon 1973). Femur with dorsal and internal faces sparsely granular; other faces smooth; dorsointernal, dorsoexternal, and ventrointernal carinae weak to moderate, granular; ventroexternal carina obsolete. Patella (Fig. 39) with external face vestigially reticulate; internal face minutely granular; dorsal and ventral faces smooth; basal tubercle strong, armed with two hook-like tubercles; dorsomedian carina moderate to weak, subgranulose; ventroexternal carina weak, smooth; ventrointernal carina weak, granular; other carinae obsolete. Chela (Figs. 40-42) with all faces weakly reticulate; dorsal marginal carina weak, granular; dorsal secondary and external secondary carinae vestigial, smooth; digital carina weak, smooth; ventromedian carina moderate, granulose; ventrointernal carina weak to moderate, smooth; internal carinae weak, weakly granular.

Legs granular, tarsomere II spine formula 5/5:5/5:6/6:6/6.

Morphometrics.—Carapace wider than long; all metasomal segments longer than wide. Pedipalp chela length/depth 2.17; pedipalp chela width/depth 0.63; pedipalp chela length/pedipalp fixed finger length 2.42; pedipalp chela length/carapace length 1.79; carapace length/pedipalp fixed finger length 1.36; pedipalp fixed finger length/pedipalp femur length 0.89; pedipalp fixed finger length/metasomal segment V length 0.87.

Comparisons.—*Diplocentrus santiagoi* differs from *D. reddelli*, *D. maya*, *D. anophthalmus*, *D. coddingtoni*, *D. lucidus*, *D. ornatus*, and *D. steeleae* by its

larger size and higher number of setae on the genital operculi (seven pairs versus two to four pairs). It differs from the troglobitic *D. mitchelli* by its lower pedipalp chela length/depth (2.17 versus 3.68), lower pectinal tooth count (12 versus 17), and the presence of pigmentation, granulation and pedipalp chelal carinae. *Diplocentrus santiagoi* can be distinguished from *D. taibeli* by its lower pectinal tooth count (12 versus 15) and the presence of reticulate costae on all faces of the pedipalp chela. It can be distinguished from *D. lourencoi* by its higher pectinal tooth count (12 versus 9 to 10), and by the granulation on the carapace and telson (smooth to weakly granular in *D. santiagoi*, dense, coarsely granular in *D. lourencoi*).

Specimens examined.—Known only from the adult female holotype.

***Diplocentrus steeleae*, new species**

Figs. 43-51

Type data.—Holotype male from La Victoria, Chiapas, México, 29 December 1944 (T. C. Schneirla), deposited in the American Museum of Natural History, New York.

Etymology.—Named in honor of my good friend and colleague, June M. Steele.

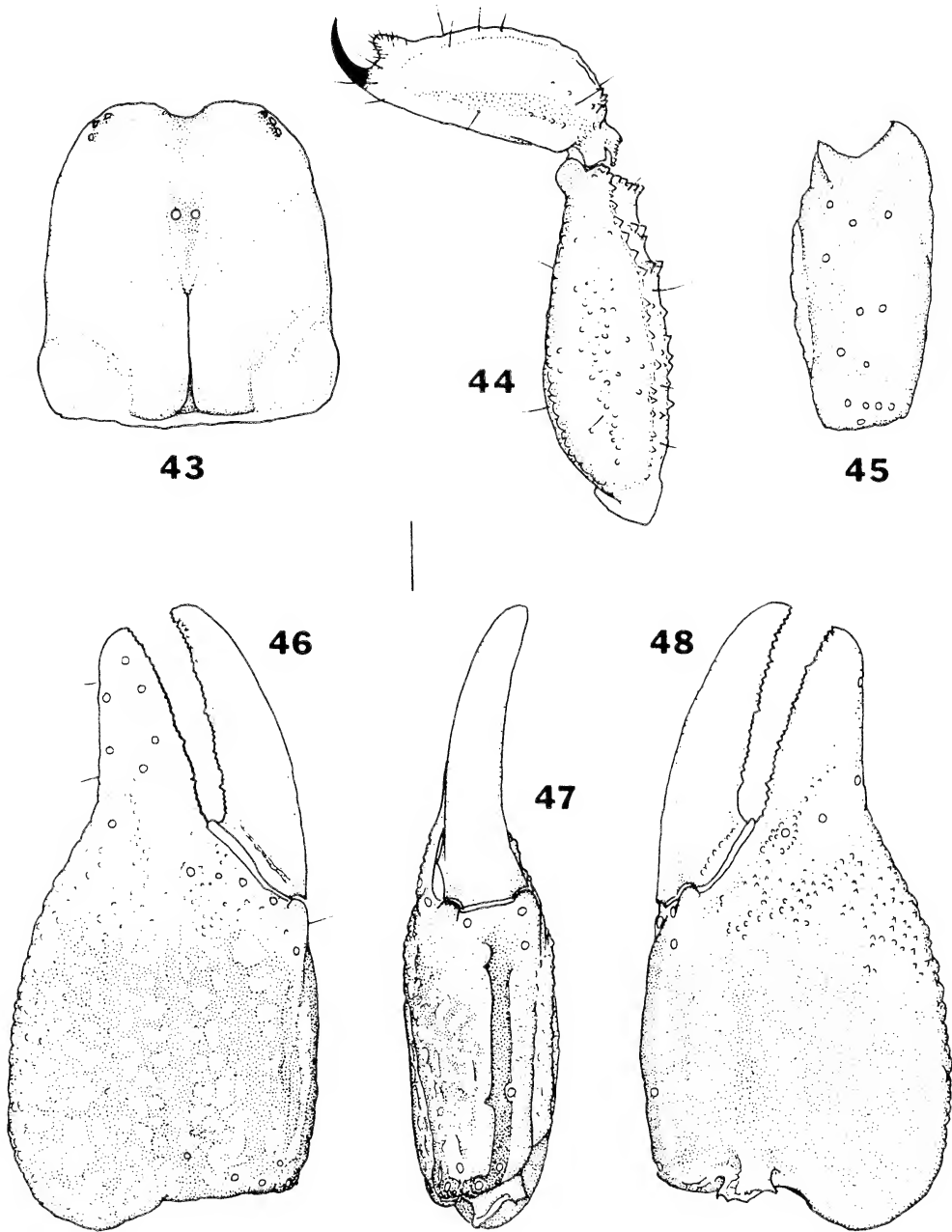
Distribution.—Known only from the type locality.

Diagnosis.—Yellowish- or reddish-brown scorpions; 25 mm in total length; carapace longer than wide, minutely granular; pectinal tooth counts 11 in males, females unknown; genital operculi with three or four pairs of setae; modal tarasomere II spine formula 4/4:4-5/5:5/5-6:6/6; males with moderately reticulate costate pattern on pedipalp; pedipalp chela length/depth 1.93; pedipalp chela width/depth 0.48.

Description.—*Male.* Color of body yellowish-brown without variable dark brown marbling (Fig. 43); pedipalps and metasoma reddish-brown. Carapace minutely granular, longer than wide; prosomal venter lustrous, punctate; pectinal tooth count 11. Genital operculi bearing three or four pairs of setae. Mesosomal tergites minutely granular; tergite VII not bilobate; submedian and lateral carinae weak, coarsely granular. Sternites smooth, lustrous; sternite VII with submedian and lateral carinae weak to vestigial, vestigially granular.

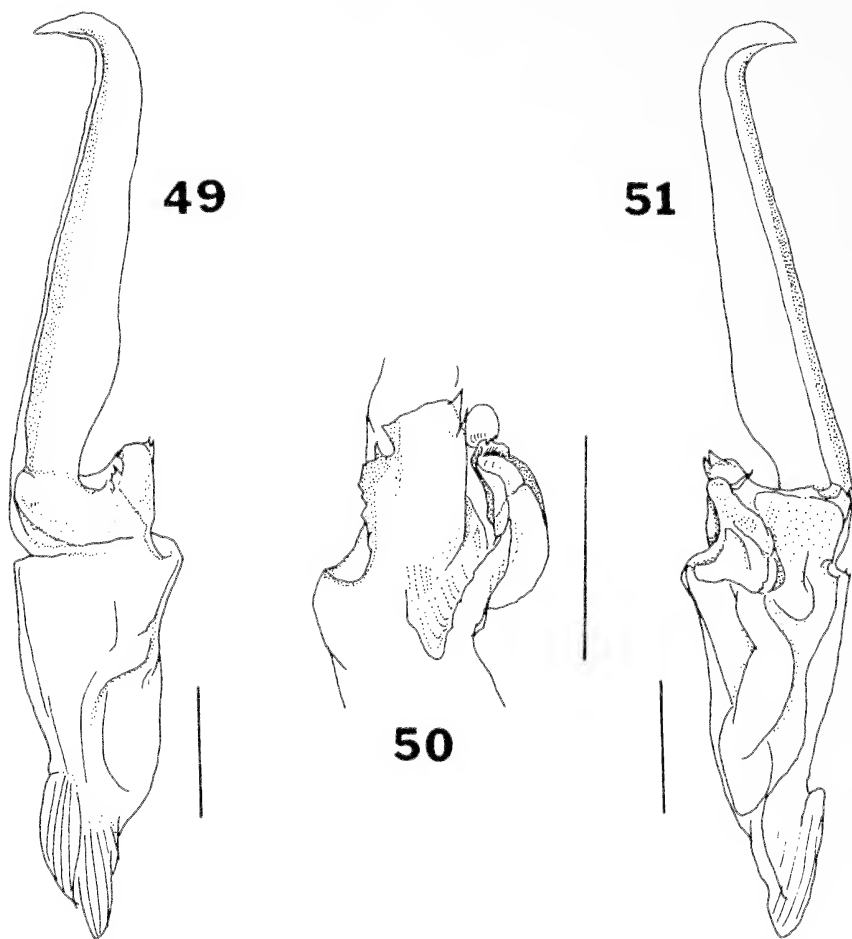
Metasoma intercarinal spaces minutely granular. Dorsolateral and lateral supramedian carinae moderate, granular on segments I-IV. Lateral inframedian carinae granular, moderately strong on segment I; weak on II and III; vestigial on IV. Ventrolateral carinae granular, moderate on segments I and II; weak on III and IV. Ventral submedian carinae moderate to weak, granular on segments I and II; weak, granular on III; vestigial, granular on IV. Metasomal segment V (Fig. 44) dorsolateral carinae weak, granular; lateromedian carinae vestigial, granular; ventrolateral, ventromedian and ventral transverse carinae moderate, tuberculate; anal subterminal carina moderate, granular; anal terminal carina obsolete. Telson (Fig. 44) granular ventrally and laterally; sparsely setose.

Pedipalps with orthobothriotaxy C (Vachon 1973). Femur with dorsal face minutely granular with a few larger granules; internal face coarsely granular; ventral and external faces minutely granular; dorsointernal carina weak to moderate, irregularly granular; dorsoexternal carina weak, irregularly granular;



Figs. 43-48.—*Diplocentrus steeleae*, new species, holotype male: 43, carapace; 44, metasomal segment V and telson, lateral aspect; 45-48, pedipalp; 45, patella, external aspect; 46, chela, external aspect; 47, chela, ventral aspect; 48, chela, internal aspect. Scale bars = 1 mm.

ventroexternal carina obsolete; ventrointernal carina weak to moderate, strongly granular. Patella (Fig. 45) with ventral and external faces weakly reticulate; internal face irregularly granular; basal tubercle moderate, with a few larger granules; dorsomedian carina moderate, reticulate; dorsoexternal, ventroexternal, and ventrointernal carinae weak to vestigial, reticulate. Chela (Figs. 46-48) with external face coarsely, moderately reticulate; internal face weakly reticulate to



Figs. 49-51.—*Diplocentrus steeleae*, new species, right hemispermatophore of holotype male: 49, dorsal aspect; 50, detail of capsular region, ectal aspect; 51, ventral aspect. Scale bars = 1 mm.

irregularly granular distally; dorsal marginal carina moderately strong, coarsely granular; dorsal secondary carina weak, smooth; digital carina moderate, smooth; external secondary carinae weak, reticulate; ventroexternal carina obsolete; ventromedian carina strong, reticulate; ventrointernal carina vestigial, smooth; internal carinae weak, reticulo-granular.

Legs minutely granular. Tarsomere II spine formula 4/4:4-5/5:5/5-6:6/6.

Hemispermatophore (Figs. 49-51) lamelliform; lateral external margin of median lobe armed with strong, sharp teeth; inner lobe with distal projection originating on the ventral margin.

Morphometrics.—Pedipalp chela of male laterally compressed. All metasomal segments longer than wide in male. Carapace longer than wide. Pedipalp chela length/depth 1.93; pedipalp chela width/depth 0.48; pedipalp chela length/pedipalp fixed finger length 2.63; pedipalp chela length/carapace length 1.77; carapace length/pedipalp fixed finger length 1.49; pedipalp fixed finger length/pedipalp femur length 0.82; pedipalp fixed finger length/metasomal segment V length 0.66.

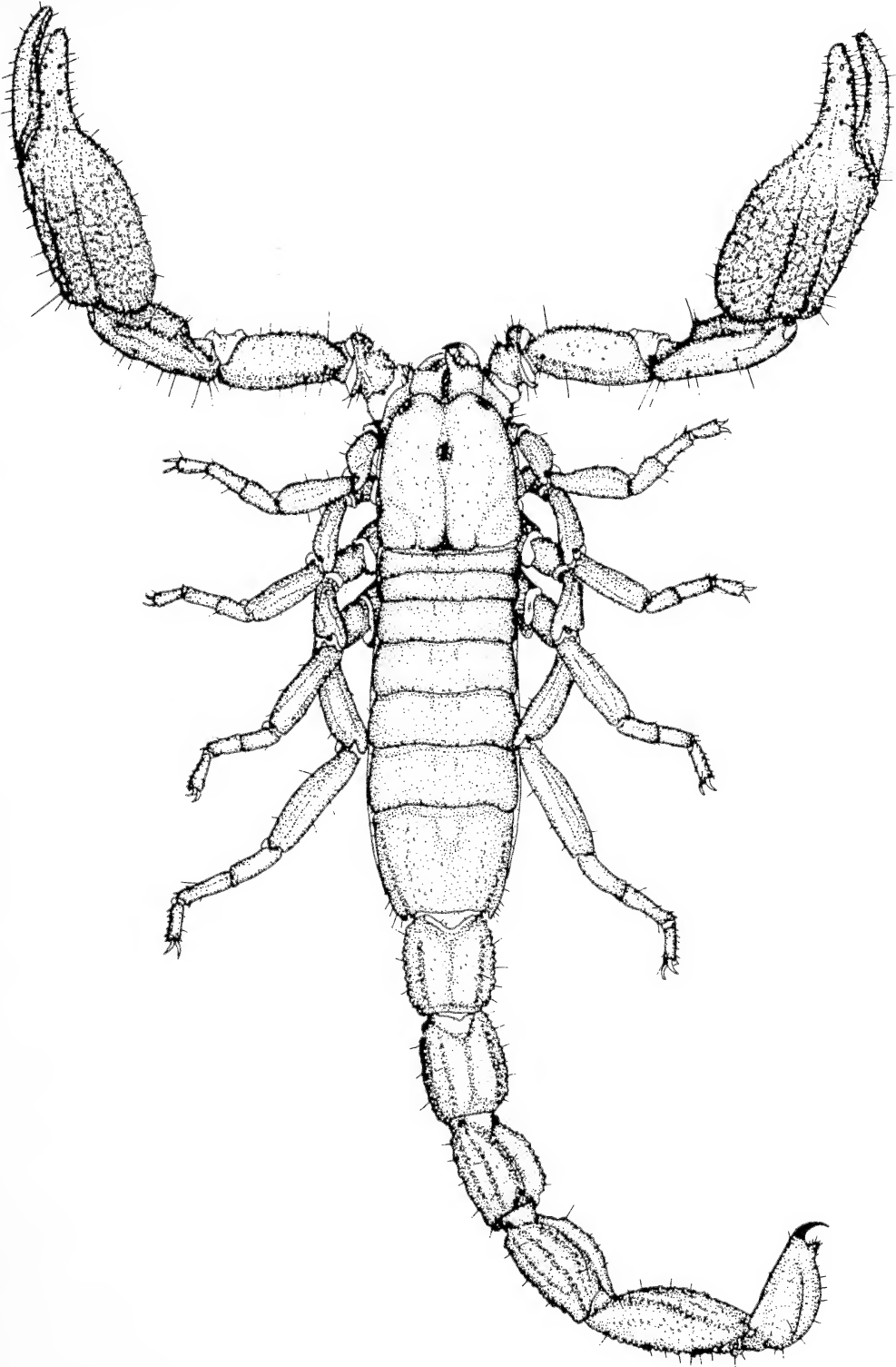


Fig. 52.—*Diplocentrus steeleae*, new species, holotype male, dorsal aspect.

Comparisons.—*Diplocentrus steeleae* can be distinguished from *D. taibeli*, *D. mitchelli*, *D. lourencoi*, and *D. santiagoi* by its smaller size and lower number of setae on the genital operculi (three to four pairs versus six to ten pairs). It differs from *D. reddelli*, *D. maya*, *D. coddingtoni*, and *D. lucidus* by its lower pedipalp chela width/depth (0.48 versus greater than 0.60) and its lack of dusky marbling on the carapace. *Diplocentrus steeleae* can be distinguished from *D. ornatus* by its lower pedipalp chela length/depth (1.93 versus 2.13-2.16), the position of the ventromedian carina of the pedipalp chela (directed between the movable finger condyles rather than towards the inner condyle), and by the presence of strong teeth on the lateral external margin of the median lobe of the hemispermatophore.

Specimens examined.—Known only from the holotype.

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DETERMINACION DE *BRYANTELLA SPECIOSA* Y *B. SMARAGDUS*, NUEVA COMBINACION, MEDIANTE LA APLICACION DE TECNICAS NUMERICAS (ARANEAE, SALTICIDAE)

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ABSTRACT

Cluster analysis by four different techniques and Prim network were performed on morphological data from 31 characters of 15 males. The results of these methods showed that there are two species involved. *Bryantella speciosa* Chickering is redescribed. *Parnaenus smaragdus* Crane is transferred to *Bryantella*, redescribed and the female described for the first time. *Parnaenus convexus* Chickering is newly synonymized with *B. smaragdus* (Crane). New records are given.

ABSTRACTO

Se realizó análisis de agrupamientos por cuatro técnicas diferentes y retículo de Prim sobre datos morfológicos de 31 caracteres de 15 machos. Los resultados de estos métodos mostraron que hay dos especies involucradas. Se redescrive *Bryantella speciosa* Chickering. Se transfiere *Parnaenus smaragdus* Crane a *Bryantella*, se redescrive y la hembra se describe por primera vez. Se sinonimiza *Parnaenus convexus* con *B. smaragdus* (Crane). Se aportan nuevas citas.

INTRODUCCION

Crane (1945) describe *Parnaenus smaragdus* sobre tres ejemplares machos: el Holotypus de Venezuela y dos Paratypi de Guyana. Incluye la especie en *Parnaenus* aclarando que por sus características debería crearse un género nuevo pero que por el cuestionable valor taxonómico de los caracteres dentro del grupo, no considera oportuno hacerlo.

Chickering (1946) describe *P. convexus* sobre un macho Holotypus y una hembra Allotypus de Panamá. En el mismo trabajo describe el nuevo género *Bryantella* con una única especie, *B. speciosa* con un macho Holotypus y una hembra Allotypus de Panamá.

Se estudiaron los lotes típicos de las tres especies y en un principio se consideró la posibilidad de que fueran conespecíficas. Los Holotipi de *P. smaragdus* y *B. speciosa* difieren en tamaño, diseño de coloración y algunas otras características pero sus palpos resultan notablemente similares. Por otra parte, el Holotypus de *P. smaragdus* comparte con el de *P. convexus* aquellos caracteres que lo diferencian de *B. speciosa* aunque la estructura de sus palpos es relativamente distinta.

Se revisó material de colecciones indeterminadas y se encontraron numerosos ejemplares que permitieron una mejor comparación. En noviembre de 1984, durante un viaje de recolección por el Parque Nacional Iguazú (Misiones-Argentina), se capturaron machos que se identificaron como *P. smaragdus* y dos hembras indeterminadas hasta ese momento. Estas hembras desovaron en el laboratorio varias veces. Se siguió el desarrollo de los juveniles hasta adultos. Se identificó entonces a la hembra de la especie dado que los machos obtenidos por crianza se determinaron como *P. smaragdus*.

La presencia, variación y combinación de determinados caracteres encontrados en todos los individuos examinados permitió la aplicación de técnicas de taxonomía numérica para la separación y delimitación de las especies involucradas. Como resultado del empleo de estos métodos, se arribó a la conclusión que *Bryantella speciosa* es una especie válida; se sinonimiza *Parnaenus convexus* con *P. smaragdus* y se transfiere esta especie al género *Bryantella*.

Abreviaturas.—OMA, OLA, OMP y OLP son ojos medios anteriores, laterales anteriores, medios posteriores y laterales posteriores respectivamente; d, dorsal; v, ventral; p, prolateral; r, retrolateral; ap, apical. Museo Argentino de Ciencias Naturales "B. Rivadavia" (MACN), Museum of Comparative Zoology (MCZ), American Museum of Natural History (AMNH), Museu Nacional de Rio de Janeiro (MNRJ), Centro de Pesquisas do Cacau (CEPEC) (Bahia, Brasil), Museu de Zoologia de la Universidade de São Paulo (MSP) y Museo Ecuatoriano de Ciencias Naturales (MECN).

METODOLOGIA

Las medidas se expresan en milímetros y fueron tomadas según Galiano (1963). La quetotaxia se cita según Platnick & Shadab (1975). La aplicación de las técnicas de taxonomía numérica se realizó según Crisci & López Armengol (1983).

En un primer intento exploratorio se incluyeron en el estudio numérico los ejemplares de colección asignables a las tres especies en cuestión, los ejemplares típicos, los obtenidos por crianza en el laboratorio y que presentaban casos extremos de variación y ejemplares de otras tres especies relacionadas que deberán ser incluidas en el género en el futuro. Se confeccionaron distintas matrices de datos variando la codificación de los estados de los caracteres desde doble estado y multiestados cualitativos y cuantitativos hasta la transformación total de los mismos en caracteres doble estado únicamente. Del mismo modo se fueron variando y eliminando individuos con el propósito de obtener distintos fenogramas.

Como a los fines del presente trabajo los distintos resultados fueron congruentes en términos de agrupaciones obtenidas, se decidió finalmente trabajar con los ejemplares típicos de las especies citadas y machos de colecciones. La variación intraespecífica encontrada en ejemplares criados en laboratorio como la inclusión en el género de otras especies serán motivo de futuros trabajos complementarios.

Los pasos seguidos en la implementación de técnicas numéricas son los siguientes:

A.—Recopilación de datos. B.—Procesamiento de los datos. C.—Análisis de los resultados.

A.—RECOPIACIÓN DE DATOS: Este paso consiste en la elección de las unidades de trabajo u OTU (*Operational Taxonomic Units*); la elección de los caracteres, registro de sus posibles estados y codificación de los mismos y la construcción de una matriz básica de datos (MBD) de OTU por estado de caracteres.

Elección de las OTUs.—Se dispuso de sesenta ejemplares aproximadamente. Se confeccionó un cuadro comparativo entre éstos y todas sus características comparables. Entre los ejemplares que presentaban igual conformación se eligió uno al azar y sus iguales fueron descartados. Se llegó así a la selección de quince ejemplares u OTUs que responden a todas las combinaciones posibles de variaciones encontradas. Sus referencias son las siguientes: OTU 1.—*Parnaenus smaragdus*, Holotypus, Venezuela. OTU 2.—*P. smaragdus*, Paratypus N°24348, Guyana. OTU 3.—*P. smaragdus*, Paratypus N°24103, Guyana. OTU 4.—*P. convexus*, Holotypus, Panamá. OTU 5.—*Bryantella speciosa*, Holotypus, Panamá. OTU 6.—Ejemplar N°8570 (MACN), Brasil. OTU 7.—Ejemplar N°8569 (MACN), Brasil. OTU 8.—Ejemplar N°8568 (MACN), Brasil. OTU 9.—Ejemplar N°8572 (MACN), Brasil. OTU 10.—Ejemplar N°8576 (MACN), Colombia. OTU 11.—Ejemplar N°8556 (MACN), Argentina. OTU 12.—Ejemplar N°8544 (MACN), Paraguay. OTU 13.—Ejemplar N°8545 (MACN), Argentina. OTU 14.—Ejemplar N°8554 (MACN), Argentina. OTU 15.—Ejemplar N°8540 (MACN), Venezuela.

Caracteres.—Durante el análisis de los individuos se encontraron catorce características morfológicas que presentaban variantes. Cada uno de los posibles estados de estas características se consideró un carácter doble estado codificándose cero (0) su ausencia y uno (1) su presencia. Se obtuvieron así treinta y un caracteres para la confección de la matriz básica de datos que son los siguientes:

a.—*Cantidad de espinas prolaterales apicales del fémur I*: Puede haber una o dos espinas.

Carácter 1: Presencia o ausencia de una espina.

Carácter 2: Presencia o ausencia de dos espinas.

b.—*Espinación de la patela I*: Puede no haber espinas o presentar una espina prolateral.

Carácter 3: Presencia o ausencia de una espina en patela I.

c.—*Dientes del promargen del quelícero*: Siempre en número de dos pueden presentarse separados o juntos emergiendo de un tubérculo común.

Carácter 4: Presencia o ausencia de dientes juntos. (Fig. 9, c).

Carácter 5: Presencia o ausencia de dientes separados. (Fig. 10, c).

d.—*Morfología del diente del retromargen del quelícero*: Este diente, robusto, cónico y curvado puede presentar su ápice gradualmente acuminado o bien oblicuamente truncado.

Carácter 6: Presencia o ausencia del diente acuminado. (Fig. 9, d).

Carácter 7: Presencia o ausencia del diente truncado. (Fig. 10, d).

e.—*Angulo dorsal apical del quelícero*: Puede presentar o no una cúspide espiniforme más o menos robusta.

Carácter 8: Presencia o ausencia de tal cúspide. (Fig. 10, e).

f.—*Tibia del palpo*: apófisis retrolateral: Puede presentar tres variantes; acuminada, larga y angosta; acuminada, corta y ancha; truncada, delgada y de longitud intermedia a las anteriores.

| Carácter | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | |
|----------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|
| OTU | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | |
| 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | |
| 3 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | |
| 4 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | |
| 5 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | |
| 6 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | |
| 7 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| 8 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | |
| 9 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | |
| 10 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | |
| 11 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | |
| 12 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | |
| 13 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | |
| 14 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | |
| 15 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | |

Fig. 1.—Matriz básica de datos. La primera fila corresponde a los números asignados a los caracteres; la primera columna indica el número de OTU; el resto de las filas indica el estado de cada carácter en cada una de las OTUs.

Carácter 9: Presencia o ausencia de apófisis acuminada larga. (Figs. 3, a; 4, a).

Carácter 10: Presencia o ausencia de apófisis acuminada corta. (Figs. 7, a; 8, a).

Carácter 11: Presencia o ausencia de apófisis truncada. (Figs. 5, a; 6, a).

g.—*Tibia del palpo*: Apófisis secundaria: Algunas tibias pueden presentar una prolongación proyectada dorsalmente sobre el cymbium, de extremo bilobado que puede ser larga y angosta o bien ancha y corta.

Carácter 12: Presencia o ausencia de una apófisis secundaria. (Ausencia: Figs. 7, b; 8, b).

Carácter 13: Presencia o ausencia de apófisis secundaria larga. (Figs. 5, b; 6, b).

Carácter 14: Presencia o ausencia de apófisis secundaria corta. (Figs. 3, b; 4, b).

h.—*Tibia del palpo*: longitud: Se encontraron tibias cortas que no sobrepasan el 30% de la longitud del cymbium, medianas que no sobrepasan el 50% y largas que sobrepasan el 50% de la longitud del cymbium.

Carácter 15: Presencia o ausencia de tibia corta (Fig. 11, j).

Carácter 16: Presencia o ausencia de tibia mediana.

Carácter 17: Presencia o ausencia de tibia larga. (Fig. 12, j).

i.—*Bulbo del palpo*: Puede ser ancho y globoso, sobresaliendo ampliamente del borde del cymbium o ser angosto, más largo que ancho, que apenas sobresale del borde del cymbium.

Carácter 18: Presencia o ausencia de bulbo ancho.

Carácter 19: Presencia o ausencia de bulbo angosto. (Fig. 12, k).

j.—*Lóbulo piriforme del bulbo del palpo*: El émbolo del palpo emerge en la porción distal del bulbo de un lóbulo piriforme invertido. Esta estructura suele ser apenas más larga que ancha pero en oportunidades es mucho más alargada.

Carácter 20: Presencia o ausencia de lóbulo piriforme corto. (Fig. 11, h).

Carácter 21: Presencia o ausencia de lóbulo piriforme largo.

k.—*Longitud del émbolo del palpo*: Los émbolos pueden ser largos, cuando describen una amplia curva de aproximadamente tres cuartos de

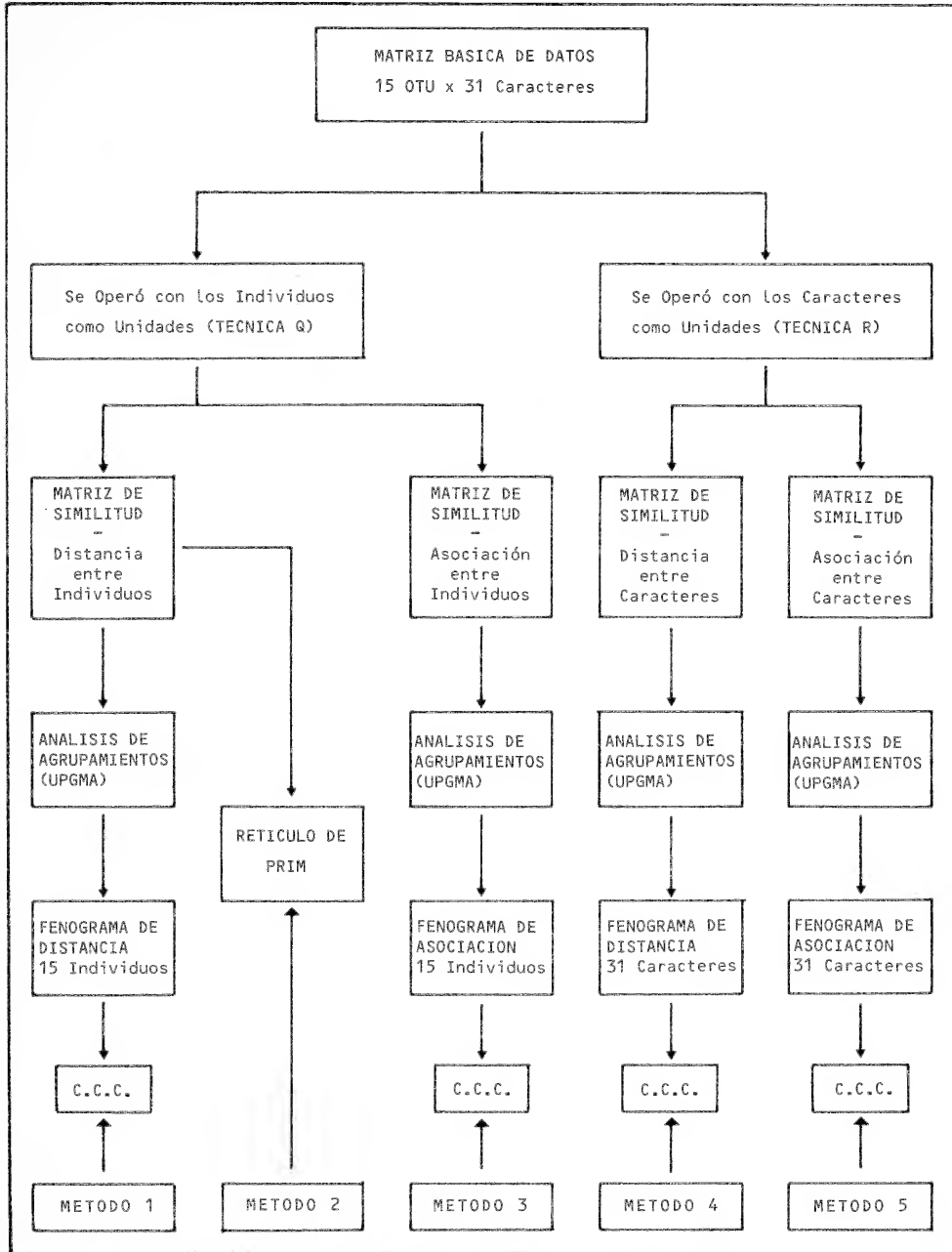


Fig. 2.—Diagrama de flujo del procesamiento de los datos.

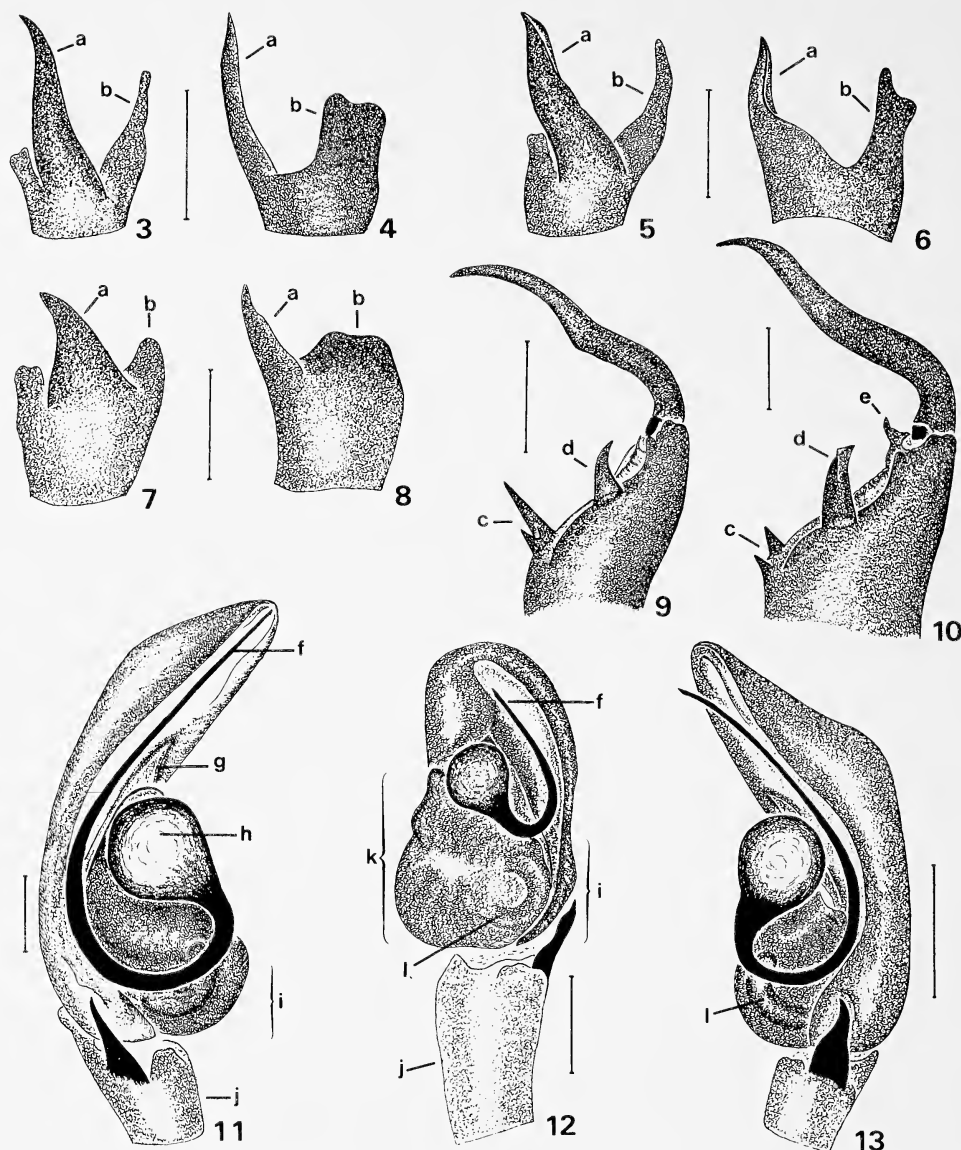
circunferencia y su ápice alcanza el borde superior del cymbium; cortos, cuando la curva descrita es apenas una semicircunferencia que no alcanza el borde superior del cymbium o medianos con características intermedias.

Carácter 22: Presencia o ausencia de émbolo largo. (Fig. 11, f).

Carácter 23: Presencia o ausencia de émbolo mediano.

Carácter 24: Presencia o ausencia de émbolo corto. (Fig. 12, f).

1.—*Distancia del émbolo a la base del bulbo*: Independientemente de la longitud del émbolo, el punto de inflexión de su curvatura parece ubicarse

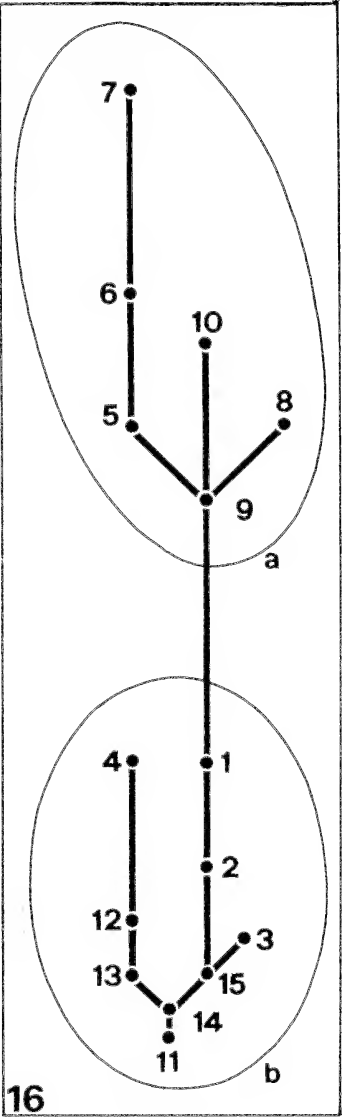
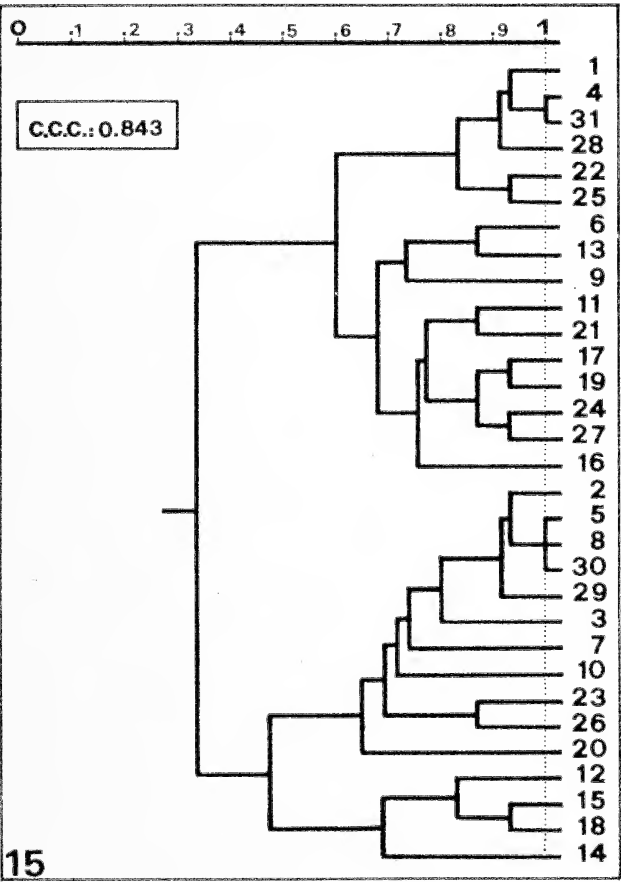
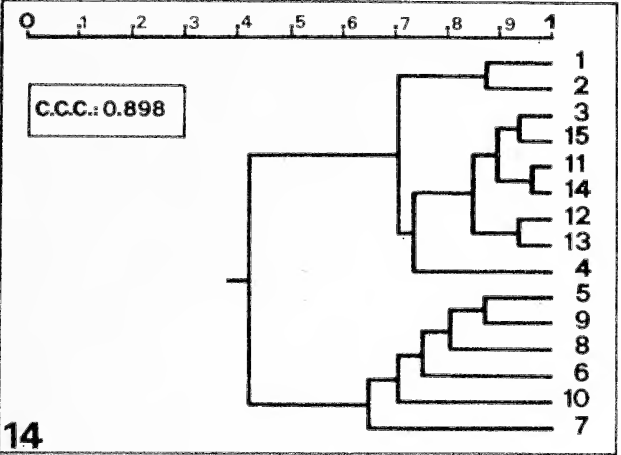


Figs. 3-13.—Caracteres taxonomicos de los machos de *Bryantella*: 3-6, 9, 13, *B. speciosa*; 3-6, tibiae de los palpos; 9, quelicero; 13, palpo (holotypus); 7, 8, 10-12, *B. smaragdus*; 7, 8, tibiae de los palpos; 10, quelicero; 11, palpo (holotypus); 12, palpo (*P. convexus*, holotypus). a = apófisis retrolateral; b = apófisis secundaria (en 7, 8, ausente); c = dientes del promargen del quelicero; d = diente del retromargen del quelicero; e = cúspide del quelicero; f = émbolo del palpo; g = carena del cymbium; h = lóbulo piriforme del bulbo del palpo; i = distancia del émbolo a la base del bulbo; j = longitud de la tibia; k = bulbo angosto; l = conducto espermático. Escala 0.2 mm.

a distintas distancias de la base del bulbo. Se consideró que la distancia es corta cuando la inflexión del émbolo pasa próxima a la base del bulbo, distancia larga cuando pasa próxima al ápice y mediana en posición intermedia.

Carácter 25: Presencia o ausencia de distancia corta. (Fig. 11, i).

Carácter 26: Presencia o ausencia de distancia mediana.



Figs. 14-16.—14, Fenograma de Asociación entre individuos (OTUs 1-4, 11-15, *B. smaragdus*; OTUs 5-10, *B. speciosa*); 15, Fenograma de Asociación entre caracteres; 16, Reticulo de Prim (a, *B. speciosa*; b, *B. smaragdus*); c.c.c, Coeficiente de Correlación Cofenética.

Carácter 27: Presencia o ausencia de distancia larga. (Fig. 12, i).
m.—Conducto espermático del bulbo: La porción visible por transparencia del conducto espermático describe una semicircunferencia cuya concavidad

puede dirigirse hacia la cara externa del bulbo o hacia el centro del mismo.

Carácter 28: Presencia o ausencia de concavidad hacia la cara externa. (Fig. 13, l).

Carácter 29: Presencia o ausencia de concavidad hacia el centro. (Fig. 12, l).

n.—*Aspecto general*: El patrón de coloración, la forma del cefalotórax y la ubicación de los OLP son caracteres asociados ya que la presencia de uno de ellos implica la presencia de los otros. Existen dos patrones que responden uno al tipo "*smaragdus*" y el otro al tipo "*speciosa*".

Carácter 30: Presencia o ausencia de aspecto "*smaragdus*". (Fig. 19).

Carácter 31: Presencia o ausencia de aspecto "*speciosa*". (Fig. 17).

Construcción de la Matriz Básica de Datos.—Una vez que se seleccionaron las OTUs y se codificaron los estados de los caracteres se construyó la MBD que se ilustra en la Fig. 1.

B.—PROCESAMIENTO DE LOS DATOS: Debido a que todos los caracteres fueron codificados en doble estado presencia-ausencia, no fue necesario estandarizar la MBD.

El análisis de los agrupamientos fue realizado mediante cinco técnicas numéricas diferentes según se ilustra en el diagrama de flujo del procesamiento de los datos de la Fig. 2.

El trabajo de computación se realizó en una computadora Epson QX-10 y los programas utilizados son una adaptación del NT-SYS (*Numerical System of Multivariate Statistical Programs*) diseñados por Rohlf, Kishpaugh & Kirk (1971).

Método 1—Técnica Q (Distancia entre individuos).—(a) Se obtuvo una matriz de similitud utilizando el coeficiente de distancia "*Manhattan Distance*" que es una modificación del "*Mean Character Difference*" propuesto por Cain & Harrison (1958) y que se expresa como la sumatoria del valor absoluto de la diferencia entre cada estado de los caracteres de cada par posible de OTUs.

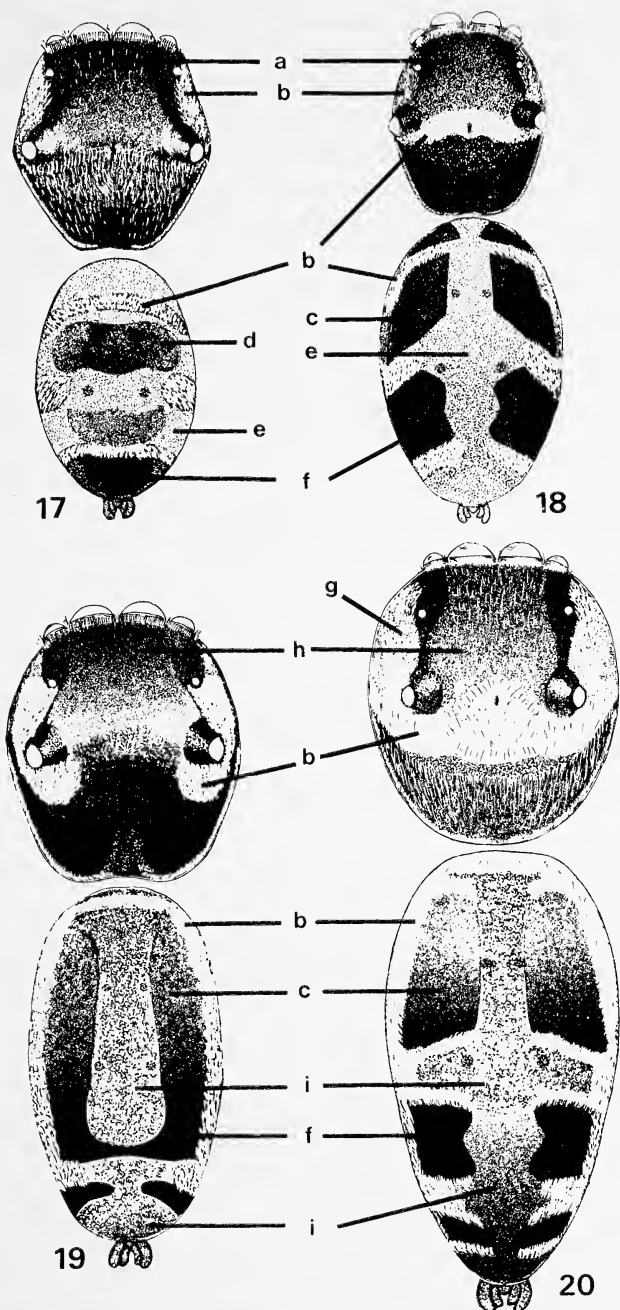
(b) Se agruparon las quince OTUs en un fenograma de distancia aplicando el método de ligamiento promedio o UPGMA (*Unweighted pair-group method using arithmetic average*) (Sokal and Michener 1958).

(c) Se calculó el "*Cophenetic Correlation Coefficient*" (c.c.c) (Sokal & Rohlf 1962) que expresa el grado de distorsión que se produce entre la matriz de similitud original y la matriz cofenética obtenidas a partir de los valores del fenograma.

Método 2—Retículo de Prim.—Aplicado a este tipo de problemas biológicos, el método ideado por Prim (1957) para problemas tecnológicos, permite obtener diagramas arborescentes en donde las distancias entre las OTUs son mínimas. A partir de la matriz de distancia obtenida en el método anterior se obtuvo el retículo de Prim que se ilustra en la Fig. 16.

Método 3—Técnica Q (Asociación entre individuos).—Se siguieron los mismos pasos que para el método 1 pero utilizando un coeficiente de asociación para la obtención de la matriz de similitud. Se aplicó el "*Simple Matching Coefficient*" (Sneath and Sokal 1973) y ligamiento promedio para el agrupamiento. Se obtuvo el fenograma de la Fig. 14.

Método 4—Técnica R (Distancia entre caracteres).—Se siguieron los mismos pasos que para el método 1, utilizando el mismo coeficiente pero considerando los caracteres como OTUs. Se obtuvo un fenograma de distancia entre caracteres.



Figs. 17-20.—Diseño dorsal: 17-18, *B. speciosa*; 17, macho; 18, hembra; 19-20, *B. smaragdus*; 19, macho; 20, hembra. a = fondo negro con iridiscencia dorada; b = escamas blancas; c = pardo rojizo oscuro opaco; d = amarillento opaco; e = iridiscencia dorada; f = negro opaco; g = escamas blancas y amarillentas intercaladas; h = fondo negro con iridiscencia verdosa; i = brillo metálico verdoso. Escala 2 mm.

Método 5—Técnica R (Asociación entre caracteres).—Siguiendo los mismos pasos que en el método 3 y con el mismo coeficiente de asociación se obtuvo el fenograma entre caracteres de la Fig. 15.

C.—ANÁLISIS DE LOS RESULTADOS: **1—Individuos.**—Los fenogramas obtenidos por distancia y por asociación son totalmente congruentes en cuanto a las agrupaciones resultantes. Se ilustra el fenograma de asociación (Fig. 14). El análisis de estos fenogramas, así como la información que brinda el retículo de Prim, evidencia la presencia de dos grupos netamente separados. El alto valor del c.c.c. indica que ha habido poca distorsión y que los resultados obtenidos son confiables. Las OTUs 1, 2, 3, 4, 11, 12, 13, 14 y 15 forman el grupo de individuos que representa a *Bryantella smaragdus* (n. comb.). La OTU 4 que es el Holotypus de *P. convexus* aparece incluida en este grupo por lo que se sinonimiza esta especie a la anterior que tiene prioridad nomenclatorial. El otro grupo formado por las OTUs 5, 6, 7, 8, 9 y 10 representa a *B. speciosa* que se mantiene como especie válida.

2—Caracteres.—En este caso también ambos fenogramas obtenidos presentan las mismas agrupaciones. Se ilustra el fenograma de asociación (Fig. 15). El c.c.c. indica poca distorsión y la información que surge es la siguiente: existen dos núcleos que presentan máxima similitud; los caracteres 4 y 31 que son diagnósticos y privativos de *B. speciosa* y los caracteres 5, 8 y 30 que lo son para *B. smaragdus*. El resto de los caracteres son variables y pueden estar presentes en una o en ambas especies. Se forman luego cuatro grandes grupos; los caracteres 1, 28, 22 y 25 asociados al núcleo 4-31 se presentan con mayor frecuencia en ejemplares de *B. speciosa*. Los caracteres 2, 29, 3, 7, 10, 23, 26 y 20 son más frecuentes en *B. smaragdus*. Los caracteres 6, 13, 9, 11, 21, 17, 19, 24, 27 y 16 son los menos frecuentes y en algunos casos corresponden a variaciones individuales de un solo ejemplar. Los caracteres 12, 15, 18 y 14 son los más frecuentes en ambas especies.

RESULTADOS Y DISCUSION

Delimitación de los taxa (Fig. 14).—De acuerdo a los resultados obtenidos por métodos numéricos se pueden diferenciar dos taxa específicos; *B. speciosa* y *B. smaragdus*.

Importancia de los caracteres (Fig. 15).—*Caracteres diagnósticos de cada taxón:* En ambas especies, los caracteres que resultaron diagnósticos para cada una de ellas no son considerados por lo general como de gran importancia taxonómica. Sin embargo, el aspecto general (especialmente el diseño de coloración), los dientes del promargen del quelícero y la presencia o no de una cúspide en el ángulo dorsal apical del quelícero, son las únicas características que permiten diferenciarlas. La genitalia de los machos, carácter considerado por muchos investigadores como el más importante para determinar especies, aquí no pudo utilizarse como diagnóstico. Un palpo aislado no podría asignarse a alguna de las especies en cuestión. No obstante, las asociaciones resultantes evidencian que la presencia de una sola espina prolateral en el fémur I, la ausencia de espinas en patela I, la concavidad del conducto espermático dirigida hacia la cara externa del bulbo y émbolos largos son caracteres más frecuentes en *B. speciosa* que en *B. smaragdus* cuyos caracteres más frecuentes son dos espinas prolaterales en fémur I, patela I con una espina prolateral, el diente del retromargen del quelícero truncado (en todos los ejemplares), la apófisis tibial del palpo acuminada y corta y los émbolos de longitud mediana.

Grupos de caracteres correlacionados: Asociación 15, 18, 12, 14 y 20: Tibia del palpo corta, bulbo ancho, de existir una apófisis secundaria ésta es corta y lóbulo piriforme corto son los caracteres más comunes en ambas especies por lo que se consideran de importancia genérica más que específica. Asociación 22-25, 23-26, 24-27: La alta asociación de estos caracteres indica que la distancia de la curvatura del émbolo al borde inferior del bulbo sería una consecuencia de la longitud del émbolo; no serían caracteres independientes como se supuso en la elección de los mismos. Asociación 6-13 y 9: Los ejemplares que tienen diente acuminado en el retromargen del quelícero, en general también presentan una apófisis secundaria larga y en ellos más frecuentemente aparece la apófisis tibial larga y espiniforme. Todos los ejemplares con estas tres características juntas son *B. speciosa*. Asociación 11, 21: Todos los ejemplares que presentan apófisis tibial truncada son *B. speciosa*, dos de ellos tienen el lóbulo piriforme del bulbo inusualmente desarrollado. Asociación 17-19, 24-27: Todos los ejemplares con tibia del palpo larga, émbolo corto y bulbo angosto son *B. smaragdus*.

Variabilidad intraespecífica.—Por lo expuesto se ve que ambas especies presentan una alta variabilidad. En *B. speciosa* la mayoría de las variaciones se presentan en quetotaxia, diente del retromargen del quelícero, apófisis tibial y secundaria del palpo. Mucha menor variación se da en genitalia, en general los émbolos son largos y el conducto espermático siempre aparece con su concavidad hacia el exterior del bulbo. En *B. smaragdus* la mayor variación se presenta en los palpos; existen ejemplares con émbolos largos, medianos, cortos y muy cortos, con bulbos anchos o angostos y el conducto espermático aparece hacia uno u otro lado. Es decir, la variabilidad se da a nivel de genitalia. Con respecto a las hembras de ambas especies se ha observado una notable constancia de caracteres con escasa variación en los conductos de los epiginos.

Interpretación evolutiva.—Haciendo una interpretación cladística de los resultados y por comparación con otras especies podría decirse que *B. speciosa* y *B. smaragdus* constituyen grupos hermanos. La divergencia habría sido reciente y es posible que *B. smaragdus* esté sufriendo un nuevo proceso de especiación. La alta variabilidad intraespecífica encontrada puede obedecer a casos de poliploidía, a altas tasas de mutación o a adaptación diferencial de las poblaciones a los distintos ambientes que habitan considerando la amplia distribución geográfica de las especies. Mejores conclusiones podrían obtenerse si se encarara un estudio sobre la biología de las especies con ejemplares provenientes de distintas poblaciones desde Panamá hasta la Argentina, con el objeto de evaluar el complemento cromosómico de los individuos, analizar homologías proteicas mediante técnicas electroforéticas, grado de interfertilidad de los individuos entre poblaciones, etc.

Género *Bryantella* Chickering, 1946

Bryantella Chickering, 1946:389 (n.gen.). Especie tipo por designación original: *B. speciosa* Chickering, 1946; Roewer 1954:1186; Brignoli 1983:626.

Aportes complementarios de la diagnosis original: Género de distribución neotropical, con individuos de talla mediana y brillo metálico. Se incluye en el grupo de las *Dendryphantae* y presenta afinidades con *Parnaenus* del que se diferencia fundamentalmente por la estructura del palpo, el área ocular plana, el

ancho máximo del cefalotórax a la altura de los OLP. No existen tubérculos oculares en los OMP y los tubérculos de los OLP no son tan prominentes como en *Parnaenus*. Los quelíceros no presentan brillo metálico.

Bryantella speciosa Chickering, 1946

Bryantella speciosa Chickering, 1946:390, figs. 343-347, (Macho Holotypus de Panamá: Canal Zone; Biological Area, agosto 1939 [Chickering] y una hembra Allotypus, julio 1939, de la misma localidad y colector, en MCZ, examinados. Un macho y dos hembras Paratypi de la misma localidad, julio 1939. Dos hembras Paratypi de Canal Zone; Forest Reserve, agosto 1939, no examinados); Roewer 1954:1186.

Diagnosis.—Se diferencia de *B. smaragdus* por su patrón de coloración y menor tamaño. En los machos, los dientes del promargen del quelícero emergen juntos de un tubérculo común, el émbolo del palpo nunca es corto, el conducto espermático con su concavidad siempre dirigida hacia la cara externa del bulbo. En las hembras, el epigino es más ancho que largo y los orificios de entrada están separados a una distancia de por lo menos tres veces su propio diámetro.

Descripción.—La descripción original es excelente. Se aportan aquí las ilustraciones del aspecto general de macho (Fig. 17) y hembra (Fig. 18), quelícero del macho (Fig. 9) y de la hembra (Fig. 26), palpo (Fig. 13), epigino (Figs. 24, 25) y tibias del palpo (Figs. 3-6).

Variaciones.—En los machos, fémur I con una espina prolateral apical (más frecuente) o dos (algunos casos); patela I sin espinas o con una espina prolateral (menos frecuente); diente del retromargen del quelícero acuminado o truncado; apófisis tibial del palpo acuminada larga, corta o truncada; apófisis tibial secundaria frecuente, larga o corta; tibia del palpo corta (un caso de tibia larga); bulbo del palpo ancho (un caso de bulbo angosto); lóbulo piriforme del bulbo corto (dos casos de lóbulo muy desarrollado).

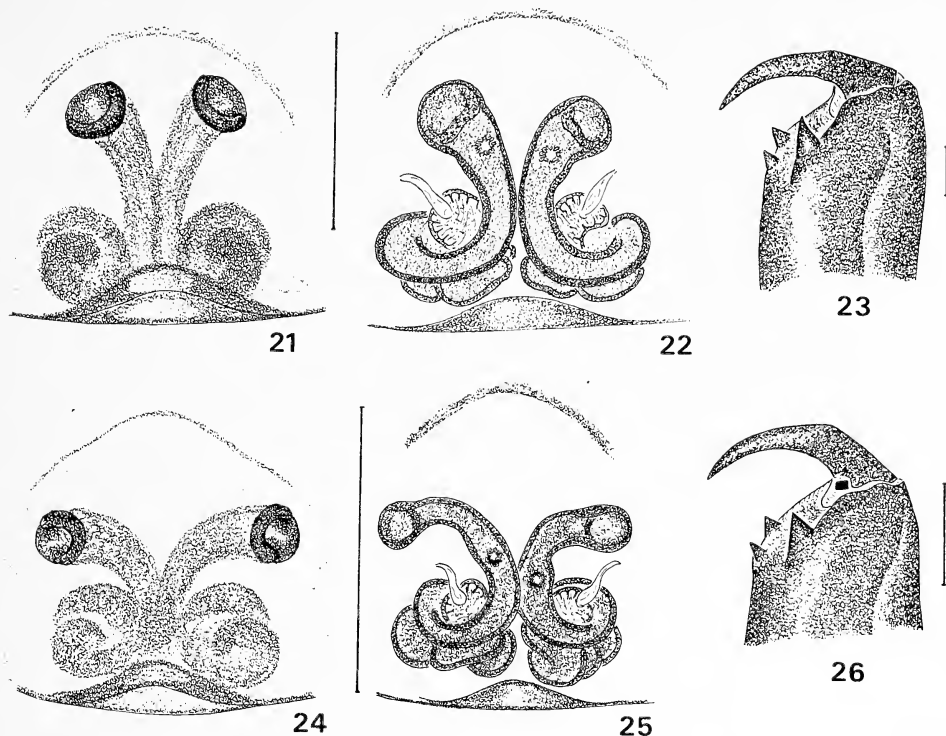
Localidad típica.—PANAMA: Canal Zone; Biological Area.

Distribución geográfica.—PANAMA. NUEVAS CITAS.—COLOMBIA: Valle del Cauca. BRASIL: Bahía: Pará: Amapá: Amazonas: Goiás.

Material examinado.—PANAMA: CANAL ZONE; Barro Colorado Island, 20 abril 1953 (A. M. Nadler), una hembra N°8575 (MACN). COLOMBIA: Valle del Cauca; Valle Cali, 1000m., (Eberhard), un macho (MCZ), 28 febrero 1973 (H. W. Levi), un macho (MCZ), un macho N°8576 (MACN). BRASIL: BAHIA; Camacán, (CEPEC), un macho N°8572 (MACN), (CEPEC), una hembra R-2137 (CEPEC), Ilheus, 12 diciembre 1969 (CEPEC), 1 hembra R-2991 (CEPEC), Faz. San Francisco, Yuçari, (CEPEC), un macho, una hembra R-2981 (MNRJ), un macho, una hembra N°8568 (MACN); PARÁ; Belem, diciembre 1971 (M. E. Galiano), un macho, una hembra (MNRJ), Utinga, julio 1970 (M. E. Galiano), un macho N°8569 (MACN), dos hembras N°8573 (MACN), Inst. Agron. Exp., febrero 1959 (A. M. Nadler), una hembra (AMNH); Ananindeua, julio 1971 (M. E. Galiano), un macho N°8570 (MACN); AMAPÁ; Serra do Navio, junio 1966 (M. E. Galiano), una hembra N°8571 (MACN); AMAZONAS; Manaus, Reserva Ducke, julio 1971 (M. E. Galiano), una hembra N°8574 (MACN); GOIAZ; Faz. Aceiro Yatai, octubre 1962 (Expedición Departamento de Zoología), una hembra E-2829 (MSP).

Bryantella smaragdus (Crane, 1945), nueva combinación

Parnaenus smaragdus Crane, 1945:40, fig. 5 (Macho Holotypus N°42472 de Venezuela: Estado de Monagas, Caripito, 29 marzo a 15 abril 1942 [J. Crane]; un macho Paratypus N°24103 de Guyana: Kartabo, 3 marzo 1924 [J. Crane] y un macho Paratypus N°24348, abril 1924 de igual colector y localidad, en AMNH, examinados).



Figs. 21-26.—Caracteres taxonomicos de las hembras de *Bryantella*: 21-23, *B. smaragdus*; 21-22, epigino; 21, vista externa; 22, vista interna; 23, quelícero; 24-26, *B. speciosa*; 24-25, epigino; 24, vista externa; 25, vista interna; 26, quelícero. Escala 0.3 mm.

Dendryphantes smaragdus: Roewer 1954:1200.

Parnaenus convexus Chickering, 1946:335, figs. 292-297 (Macho Holotypus de Panamá: Canal Zone, Biological Area, julio 1943) marzo 1944 [Zetek] y una hembra Allotypus con iguales referencias, en MCZ, examinados. Dos Paratypi, de la misma localidad, junio—julio 1939, no examinados) NUEVA SINONIMIA.

Dendryphantes convexus: Roewer 1954:1192.

Diagnosis:—Se diferencia de *B. speciosa* por su patrón de coloración y mayor tamaño. En los machos, los dientes del promargen del quelícero emergen separados, existe una cúspide espiniforme en el ángulo dorsal apical del quelícero. En las hembras, el epigino es más largo que ancho y los orificios de entrada están separados a una distancia no mayor de dos veces su propio diámetro.

Descripción.—Medidas del macho Holotypus: Largo total 5.99. Prosoma: largo 2.7, ancho 2.53, alto 1.67. Clípeo: alto 0.08. Estría torácica entre los OLP. Area ocular: largo 1.67; ancho hilera anterior 1.76, ancho hilera posterior 2.23; distancia OMP-OLA 0.33; distancia OMP-OLP 0.83; diámetro OMA 0.58; diámetro OLA 0.28. Quelíceros (Fig. 10). Esternón: largo 1.27, ancho 0.77. Patas: 1-4-2-3. Quetotaxia: Fémures: I d 1-1-1, p ap 2; II, III, IV d 1-1-1, p ap 2, r ap 1. Patela I p 1. Tibias: I v 2-2-2; II, IV v 1r-2; III v ap 2, p 1, r 1. Metatarsos: I, II v 2-2; III v ap 2, p ap 2, r ap 2; IV v ap 2, p ap 1, r ap 1. Palpo (Fig. 11). Abdomen: largo 2.37, ancho 1.73.

Coloración en vivo.—Macho N° 8556 (MACN): Patas, quelíceros, piezas bucales, esternón, cefalotórax y vientre negros. Los dos últimos cubiertos por pequeñísimas escamas iridiscentes verdosas. Diseño dorsal (Fig. 19).

Variaciones y otras características.—Los machos de la especie presentan siempre dos espinas prolaterales apicales en fémur I, una espina prolateral en patela I y el diente del retromargen del quelícero truncado. La longitud de la tibia del palpo es variable desde muy corta a muy larga; las apófisis tibiales son en general acuminadas cortas (algunos casos de acuminada larga pero no se hallaron apófisis truncadas); frecuentemente sin apófisis secundaria (presente en algunos ejemplares, siempre corta); el bulbo del palpo puede ser ancho o angosto; el émbolo de longitud mediana en la mayoría de los casos, puede variar desde muy largo a extremadamente corto; el conducto espermático puede ubicarse hacia el borde del bulbo o hacia el centro sin frecuencias mayoritarias para alguno de los casos (Figs. 7, 8, 10, 11, 12).

Descripción de la hembra N°8557 (MACN).—Medidas.—Largo total 8.51. Prosoma: largo 3.86, ancho 2.93, alto 1.73. Clípeo: alto 0.07. Estría torácica entre OLP. Area ocular: largo 1.77; ancho hilera anterior 2.0; ancho hilera posterior 2.67; distancia OMP-OLA 0.56, distancia OMP-OLP 0.9; diámetro OMA 0.6; diámetro OLA 0.3. Quelíceros (Fig. 23). Esternón: largo 1.33, ancho 0.83. Patas 1-4-2-3. Quetotaxia: Fémures: I, II d 1-1-1, p ap 2; III d 1-1-1, p ap 2, r ap 1; IV d 1-1-1, r ap 1. Tibias: I v 2-2-2; II v 1r-2; III v ap 2, r 1; IV v ap 2. Metatarsos: I, II v 2-2; III, IV v ap 2, p ap 2, r ap 1. Abdomen: largo 5.19, ancho 3.1. Epigino (Figs. 21, 22).

Coloración en vivo.—Patas, quelíceros, piezas bucales y esternón negros. Cefalotórax negro cubierto por pequeñísimas escamas iridiscentes verdosas; por sobre éstas numerosos pelos blancos y amarillentos intercalados. Vientre negro con reflejos iridiscentes verdosos. Diseño dorsal (Fig. 20).

Localidad típica.—VENEZUELA: Monagas; Caripito.

Distribución geográfica.—VENEZUELA: Monagas. NUEVAS CITAS.—PANAMA: Canal Zone. VENEZUELA: Anzoátegui. COLOMBIA: Putumayo. ECUADOR: Napo. BRASIL: Goiás: Amazonas. PARAGUAY: Caazapá: San Pedro. ARGENTINA: Misiones: Chaco: Salta: Jujuy: Entre Ríos.

Material examinado.—PANAMA: CANAL ZONE; Barro Colorado Island, agosto 1928 (A. M. Chickering), un macho (AMNH). VENEZUELA: ANZOATEGUI; San Tomé, (T. Briceno Baaz), un macho N°8540 (MACN). COLOMBIA: Putumayo; Buena Vista, 23-29 julio 1972 (W. Eberhard), un macho N°8543 (MACN). ECUADOR: NAPO; Limoncocha, 2 abril 1983 (L. Avilés), un macho N°83-28 (MECN). BRASIL: GOIAZ; Faz. Aceiro Yatai, octubre 1962 (Expedición Departamento de Zoología de San Pablo), una hembra N°8541 (MACN): AMAZONAS; Manaus, Reserva Ducke, julio 1971 (M. E. Galiano), una hembra N°8542 (MACN). PARAGUAY: CAAZAPÁ; Pastoreo, (D. Wees), una hembra (MCZ): SAN PEDRO; San Estanislao, enero 1947 (Bridarolli-Williner), un macho N°8544 (MACN). ARGENTINA: MISIONES; San Javier, San Javier, diciembre 1948 (Birabén), un macho N°8545 (MACN), diez machos, cinco hembras N°8546 (MACN), dos machos, dos hembras (MCZ); Iguazú, Parque Nacional Iguazú, noviembre 1986 (M. E. Galiano), una hembra N°8547 (MACN), octubre 1978 (M. E. Galiano), dos machos, dos hembras N°8549 (MACN), octubre 1979 (M. E. Galiano), una hembra N°8552 (MACN), noviembre 1984 (C. L. Scioscia), un macho N°8556 (MACN), un macho N°8557 (MACN), una hembra N°8558 (MACN) (descendencia: veinticuatro machos, veintidós hembras), una hembra N°8559 (MACN) (descendencia: nueve machos, seis hembras), Puerto Libertad, noviembre 1945 (Prosen), un macho N°8548 (MACN), noviembre 1948 (Birabén), un macho, una hembra N°8551 (MACN), Ruta 12-Río Uruguay, febrero 1951 (Giai-Partridge), dos hembras N°8550 (MACN), Puerto Bosetti, enero 1964 (Viana), un macho N°8553 (MACN); Concepción, Santa María, octubre 1944 (Viana), un macho N°8554 (MACN), octubre 1943 (Viana), una hembra N°8555 (MACN); Oberá, Oberá, noviembre 1986 (M. E. Galiano), una hembra N°8564 (MACN): CHACO; Bermejo, Selva del Río de Oro, enero 1965 (M. E. Galiano), una hembra N°8560 (MACN): SALTA; Gral. José de San Martín, Tartagal, marzo 1961 (A. Bachmann), un macho N°8563 (MACN), Quebrada de Piquirenda, octubre 1966 (Hepper), un macho N°8561 (MACN); Cafayate, Río Santa María, julio 1947 (Giai), un macho N°8562 (MACN): JUJUY; Ledesma, Ledesma, noviembre 1978 (Williner), un macho N°8565 (MACN), Yuto, El Pantanoso,

octubre 1967 (M. E. Galiano), una hembra N°8566 (MACN): ENTRE RÍOS; Concordia, Salto Grande, marzo 1964 (M. E. Galiano), un macho N°8567 (MACN).

Observaciones.—*Con respecto a la publicación original:* El Paratypus N°24103 no es un ejemplar inmaduro; es un macho adulto. La estructura descrita por Crane como una espina delgada que surge por detrás del bulbo del palpo en los machos, es en realidad una carena en forma de V invertida de la cara interna del cymbium que bordea la cavidad donde se aloja el bulbo (Fig. 11, g).

Con respecto a la hembra Allotypus de P. convexus: El ejemplar está muy depilado y el abdomen casi destruido. Por sus características se evidencia que pertenece al género *Bryantella* pero por la estructura del epigino no se puede asegurar que pertenezca a la especie y por lo tanto no se redescrive. El ejemplar descrito como hembra de la especie en este trabajo fue capturado vivo y se tuvo comprobación empírica en bioterio para tal designación.

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WHY DO "FAMILY SPIDERS", *STEGODYPHUS* (ERESIDAE), LIVE IN COLONIES?

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ABSTRACT

In the social eresid spider *Stegodyphus mimosarum*, most individuals under natural conditions live in colonies containing up to several hundred individuals. Female size at maturity is reduced in large colonies as is the number of eggs produced per female. This reduction of female fecundity seems to result from increasing competition over food as the number of females in a colony increases, and is interpreted in terms of a "constraint" model for group living proposed by Emlen (1984).

INTRODUCTION

Cooperative societies have arisen independently in several taxa of spiders. Since social spiders cooperating in predation regularly capture larger prey than solitary spiders of a similar size, it is generally assumed that the greater ease with which prey can be caught and killed by a group accounts for communal hunting and has promoted the evolution of social life in spiders (Brach 1977; Buskirk 1981; Nentwig 1985). But studies performed in the field and in our laboratory on *Stegodyphus mimosarum* Pavesi, one of the most social spider species, have shown that (1) the increase in prey availability does not keep pace with increasing spider numbers and feeding becomes less efficient as group size increases; (2) colony members compete over food, the more so the larger the colony; (3) spiders from larger colonies are smaller than those from smaller colonies; and (4) most colonies are larger than are optimal for individual spider's growth (Ward and Enders 1985; Ward 1986). On the other hand, spider reproductive output is a function of the intake of prey biomass, and fecundity correlates with spider size (Craig 1987). To answer the obvious question, how group-living affects female fecundity in *S. mimosarum*, we determined the numbers of egg-cocoons, and the numbers of eggs in them, for colonies of different sizes.

MATERIAL AND METHODS

Stegodyphus mimosarum, locally known as "family spider", inhabits African dry thornbush country, living in colonies in compact, sponge-like silk nests with tubular passages inside which the spiders tend to remain during the day. One or more trap sheet-webs carrying very adhesive cribellar silk are attached to the nest and stretch to nearby twigs, catching a variety of insects. The species reproduces

between November and March and has an annual life cycle (Seibt and Wickler 1988).

For an analysis of the nest contents and of the composition of colonies we collected 56 *S. mimosarum* nests during Nov./Dec. in the years 1982, 1984 and 1985 from eastern Transvaal and north-eastern Natal (South Africa). The nests were carefully dissected and all inhabitants (a total of 2298 females and 249 males) counted and measured. Size of the live individuals is given as total body length (prosoma plus opisthosoma), measured to ± 0.1 mm with a vernier calliper. Female sexual maturity was checked from the external appearance of the epigynal opening (following O. and M. Kraus 1988). We refer to the number of female spiders living in a given nest as "colony size". Males are omitted as they occurred in very low numbers and do not spin trap webs. Statistical tests used were Spearman's coefficient of rank correlation r_s , Pearson's correlation coefficient r , Mann-Whitney U -test, Student's t -test, all following Sokal and Rohlf (1981).

RESULTS

Female size at maturity.—Colony size varied between 1 and 372. Even with the unaided eye it was apparent that mature females from large colonies were smaller than those from small colonies. We measured 29 mature females from a colony containing 42 females and they were 8.4 ± 0.6 mm (mean \pm SD) long. Also measured were 105 females from the largest colony (372 females) which had an average length of 6.5 ± 0.7 mm. The difference is highly significant (t -test, $p < 0.0001$).

Numbers of eggs and of cocoons.—Eggs of *S. mimosarum* are about 0.5 mm in diameter. They are deposited in flat, circular cocoons of about 5 mm diameter.

Egg numbers for 32 cocoons, taken from 7 colonies, ranged from 15 to 48. The average egg number per cocoon was $26.3 (\pm 8.6)$. No counts are available for colonies containing more than 30 females. For smaller colonies, the number of eggs per cocoon decreases with increasing colony size (Fig. 1a). Taking all 32 counts as independent data, the decrease is significant ($r_s = -0.448$, $p = 0.01$); the average egg number per cocoon for each colony still gives a negative, though a non-significant $r_s = -0.5455$ ($n = 7$).

In 29 nests we found between 1 and 20 egg cocoons per nest. There was no significant correlation between the number of cocoons and the number of either all females ($r_s = 0.316$, $p = 0.095$), or only mature females ($r_s = 0.419$, $p = 0.074$), in a colony.

Thus, neither the number of eggs per cocoon nor the number of egg cocoons present increases significantly with the number of females (mature, or all) in a colony. Even when we neglect a possible tendency towards reduced egg number per cocoon in larger colonies, the per capita reproductive output, as indicated by the ratio of cocoons per female over number of females in the colony (Fig. 1b) suggests an exponential decrease. Indeed a log-log-transformation gives a significant negative linear regression (Pearson $r = -0.772$; $p < 0.0001$) which fits the data significantly better than a linear regression with the untransformed data ($r = -0.434$; $p = 0.019$); the difference between the correlation coefficients is significant ($p < 0.05$; $x = 4.084$; $df = 1$. Sachs 1969). We conclude, therefore, that an individual's expected reproductive output shows a constant allometric decline with increasing colony size.

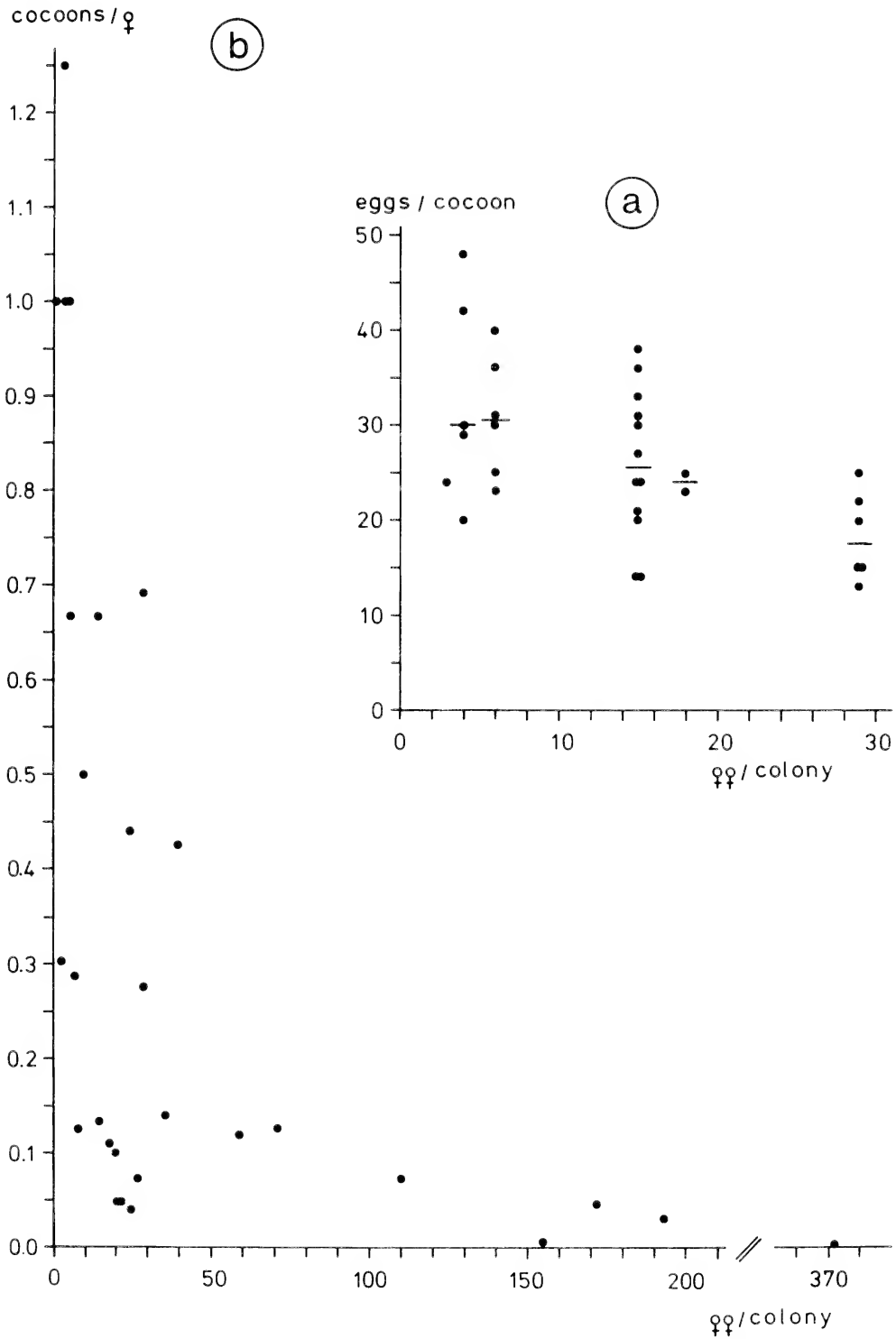


Fig. 1.—Number of eggs per cocoon (a) and of cocoons per female (b) for different colony sizes of *Stegodyphus mimosarum*. Horizontal bars in a indicate the median.

This fact refers to the reproductive output measured at a given time. In theory, larger colonies, or at least a considerable fraction of their female population, might reproduce later, and the number of cocoons present at the time of collection might be a less reliable measure of the total number of cocoons produced for larger than for smaller colonies. We therefore compared our chances of finding cocoons in small and large colonies. We divided the total of 56 colonies analyzed into two sets according to whether they contained cocoons (29 colonies) or not (27 colonies). Sizes of colonies with cocoons (median 21 females, range 1-372, quartiles 7.5 and 49.5) did not differ significantly from sizes of colonies without cocoons (median 12, range 1-351, quartiles 4.0 and 25.0); *U*-test, $p = 0.09$. But colonies with cocoons tended to be larger rather than smaller compared to colonies without cocoons.

DISCUSSION

All colonies analyzed were long-established ones, as could be seen from the perfect nest construction. Immigration of individuals into established colonies has never been reported and is highly unlikely in view of the colony distribution in the field. A rich local food supply seems to relate to a higher number of colonies in a given patch rather than to an increase in colony size (Seibt and Wickler 1988). Colony growth seems to result from reproduction over successive generations only. But even if an increase in colony size was favored by prey availability, individual spider size obviously does not keep pace, as shown by the size of the mature females in the colonies. Although females may emigrate to start new colonies, the largest females tend to stay in the nests while intermediate-sized individuals are more likely to leave, as Ward (1986) found with experimental *S. mimosarum* colonies.

Smaller body size of mature females in larger colonies is in line with Ward's (1986) finding that as nest size increases, the mean weight of the spiders (not checked for maturity) decreases. This is best understood as a consequence from competition which increases with group size.

Competition over food is easily observed in *Stegodyphus*. The seemingly cooperative subduing of prey, where several spiders grab one insect appendage each and pull backwards, making it impossible for the insect to struggle free, results from each spider's tendency to secure the whole prey for itself; small prey items are in fact carried home by a single spider, as are parts of a larger item should it break into pieces. In the laboratory, spiders in smaller groups were more cooperative and less competitive than those in larger groups (Ward 1986), and feeding became less effective as group size increased (Ward and Enders 1985). This suggests that indeed there is a smaller amount of food available to each spider as colony size increases.

In a recent synopsis of available data, Craig (1987) states that (a) within-species variation in spider size at sexual maturity seems to be a function of local variation in food availability, and (b) spider reproductive output is a function of the intake of prey biomass. As shown here, mature *S. mimosarum* females taken from a large and a small colony differ in average size by more than 2 mm. It seems unlikely that a spider can increase its total length by 1/4 or 1/3 after having reached sexual maturity. Thus we assume that mature females in a large

colony could never attain the size of females in a small one. And as the cocoon counts show, smaller body size of females in larger colonies seems to be linked to lower fecundity as a result from sociality.

Admittedly, the exact amount of reduction in reproductive output caused by social life cannot be assessed at present since it partly depends on the consequences of kin association which is only superficially known for *Stegodyphus*. Also, lowered total offspring number could be compensated by lowered offspring mortality, i.e., reproductive output times the probability that offspring become adults may be the relevant measure, as shown by Smith (1982) for the facultatively communal spider *Philoponella oweni* (Chamberlin) (Uloboridae). Riechert (1985) could rule out the necessity to subdue prey jointly as an explanation for living socially in the spider *Agelena consociata* Denis (Agelenidae); she also found that foraging success and egg production decrease with increasing group size in this species. Originally, Kullmann (1968) suggested that the construction of a safe retreat is a first step toward sociality in spiders; he listed some permanent social species, e.g., *Philoponella republicana* (Simon), which only build communal retreats but catch prey individually.

There are good reasons to assume that *Stegodyphus* offspring benefits from a considerable degree of safety in a large existing nest. Social *Stegodyphus* spiders, by their combined spinning activities, construct a very dense and compact nest. Young spiders hatched in a colony nest usually stay there. Nests are occupied and enlarged by consecutive generations of spiders and may finally attain the size of more than a man's head, acting as protective shields against predators, solar radiation, and presumably also against excessive water loss. Physical protection in a carton-like nest against wind and fire seems to be an important factor facilitating social behavior also in *Diaea* sp. (Thomisidae) (York Main 1986). Individuals emigrating from a *Stegodyphus* colony would seem to be in great danger from predators, as shown for the comparable social spiders *Anelosimus eximus* (Vollrath 1982) and *Agelena consociata* (Riechert et al. 1986). High costs or risks associated with departure seem to operate as constraints, tipping the cost-benefit balance against the choice of personal reproduction in many social groups of cooperatively breeding birds and mammals (Emlen 1984). Available data suggest that this also applies to social *Stegodyphus* and possibly to other social spiders, regardless of whether their sociality evolved via individual, kin or group selection, the latter being proposed by Lubin (1984/85) and Aviles (1986).

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SOUND PRODUCTION AND ASSOCIATED MORPHOLOGY IN MALE JUMPING SPIDERS OF THE *HABRONATTUS AGILIS* SPECIES GROUP (ARANEAE, SALTICIDAE)

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ABSTRACT

Stridulating male jumping spiders in the *Habronattus agilis* species group have a file on the back of the cephalothorax and stout, curved setae on the front of the abdomen. Compared to non-stridulating *Habronattus* species, stridulators have modified sclerites around the pedicel, and much more massive muscles running from the lorum to the dorsal carapace apodeme and from the side of the pedicel to the epigastric plate. Sound mostly below 3500 Hz is produced during courtship when the abdomen is vibrated up and down against the back of the carapace. When most of the scraper setae are ablated, the sound is diminished. Stridulation may have evolved from the common salticid behavior of abdomen twitching.

INTRODUCTION

The well-sighted jumping spiders often appear to communicate primarily by vision, with striking ornaments and complex courtship motions, yet recently stridulation with probable communicatory function has been reported in three genera. Male *Phidippus mystaceus* (Hentz) have a plectrum on the palpal tibia which rubs against a file on the cymbium during courtship (Edwards 1981). In *Saitis michaelseni* Simon, males scrape stout setae on the front of the abdomen against a file on the back of the carapace (Gwynne and Dadour 1985). A very similar mechanism had been earlier described in *Habronattus agilis* (Banks) and its relatives by Maddison (1982, reported as *Pellenes agilis*), on whose preliminary report we here elaborate.

Habronattus agilis and other species in the *agilis* species group (see Griswold 1987:181) live in sandy habitats in North America, usually on grass tufts, other vegetation, and dry leaves. Males have distinctive vertical fringes on the first legs

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which are exposed during courtship (Fig. 1). The following species in the group were studied by us: *H. agilis* (Banks), *H. alachua* Griswold, *H. cognatus* (Peckham and Peckham), *H. conjunctus* (Banks), *H. elegans* (Peckham and Peckham), *H. georgiensis* Chamberlin and Ivie, and *H. peckhami* (Banks). Five additional species in different species groups were also studied: *H. borealis* (Banks), *H. americanus* (Keyserling), *H. oregonensis* (Peckham and Peckham), *H. calcaratus* (Banks), and *H. decorus* (Blackwall).

MATERIAL AND METHODS

Collecting localities.—*H. cognatus* specimens were collected on Long Point, Lake Erie, Ontario (SEM's, sclerites, musculature), Bruce Beach, Lake Huron, Ontario (sclerites), Warren Dunes State Park, Michigan (behavior recordings and experiments). The other *agilis*-group specimens were: *H. agilis*, from Crane's Beach, Essex Co., Massachusetts (behavior); *H. conjunctus*, from Grays Well Road, east of El Centro, Imperial Co., California (behavior recordings); *H. elegans*, from Chilao Campground, Los Angeles Co., Quail Lake, Los Angeles Co., and Camarillo, Ventura Co., all from California (behavior recordings); *H. alachua*, from Ocala National Forest, Marion Co., Florida (behavior, SEM); *H. peckhami*, from Stinson Beach, Marin Co., California (behavior). *H. borealis* specimens were from the Hamilton Beach Strip, Hamilton, Ontario (SEMs, sclerites, musculature), Long Point, Ontario (musculature), and Warren Dunes State Park (behavior). *H. americanus* were from Nevada City, Madison Co., Montana (sclerites), Austin, Nevada and Beaver Creek, Gunnison Co., Colorado (musculature) and South Fork Campground, San Bernardino Mts., California (behavior), *H. calcaratus maddisoni* Griswold from Rigaud, Quebec (musculature, sclerites), *H. decorus* from Pulaski Park, Delta Co., Michigan (sclerites) and Gull Lake, Alberta (musculature), and *H. oregonensis* from Furry Creek, British Columbia (musculature) and the Nacimiento-Fergusson Road, Monterey Co., California (behavior). Specimens were identified by the senior author with the aid of information, unpublished at the time, from Charles Griswold (see Griswold 1987).

Morphology.—Males to be examined with a scanning electron microscope (SEM) were first critical-point-dried. To observe sclerites, internal tissues were digested in pepsin for a few days and fully cleared overnight in cold 1 N KOH. To understand musculature, numerous dissections were made of specimens of *H. borealis* and *H. cognatus* fixed in Kahle's solution, along with a few dissections of alcohol-fixed *H. borealis*, *cognatus*, *calcaratus*, *americanus*, *oregonensis*, and *decorus*. Figures 6 and 8 were done with a camera lucida on an Olympus BH2® brightfield compound microscope from paraffin-dipped specimens sectioned by hand with a razor blade and mounted in Euparal, supplemented with information from the dissections and other sections. Figures 7 and 9 were done of muscles in alcohol with the same camera lucida and microscope with incident fiber-optics light.

Behavior and sound.—Courtship behaviors were videotaped for 4 males of *H. cognatus*, 3 of *H. elegans*, 3 of *H. conjunctus*, 2 of *H. oregonensis*, and one male each of *H. borealis* and *H. americanus*. All videotaping was done in a sound-treated 23–24°C room courtesy of the Speech and Hearing Department of Bradley

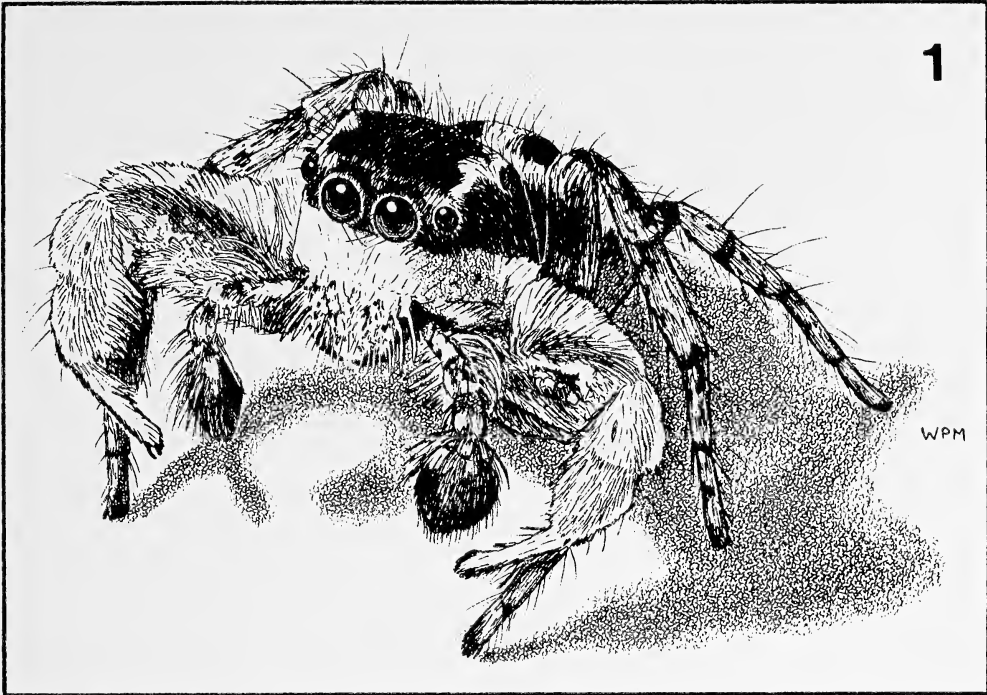
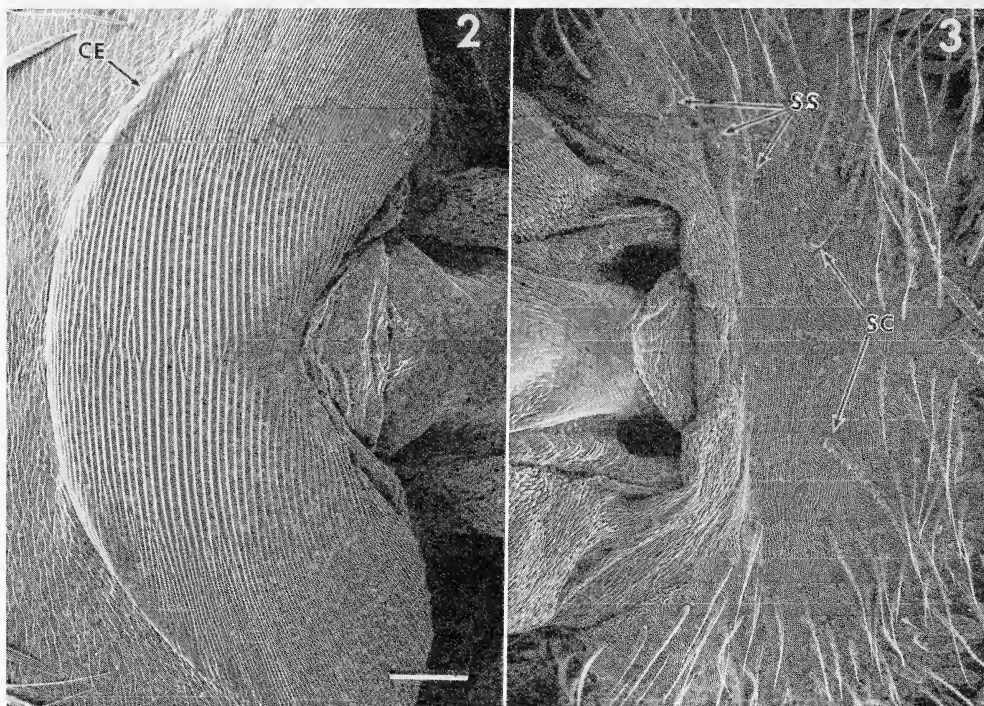


Fig. 1.—Male *Habronattus cognatus* in courtship pose (from Uetz and Stratton 1983; used by permission of Pergamon Press).

University. Video recordings were made with a JVC color video camera (Model 6X-N74 with 105 mm macro lens) connected to a Pentax Video Recorder (Model PV-R1000A). Sound recordings were made of spiders placed on a light piece of cardboard (22 X 16.5 cm) taped over a Pressure Zone Microphone® (“Sound Grabber”™, Crown International, Inc.), connected to the videorecorder. The cardboard acted as a sounding board, as might dry leaves in the spider’s natural habitat. We did not attempt to isolate a substrate-borne component of the sound. The videotapes were used to determine durations and frequencies of some of the prominent behaviors. Sounds recorded on the videotapes were rerecorded on cassette tape and analyzed using a Kay Elemetrics Sonagraph® model 6061B.

Ablation experiments.—Ablation operations were performed to investigate the importance of the prominent setae on the front of the abdomen. In two males (#1 and #2) of *H. cognatus* the two largest “scraper” setae above the pedicel were scraped off with a microscalpel while the spider was CO₂-anesthetized in an operation lasting about five minutes. One other male (#3) was anesthetized and sham operated. After about three hours, recordings were made from all males. Later the same day, a second operation was performed in the same manner on the two previously-operated males, to remove some of the smaller “scraper” setae beside the pedicel on the front of the abdomen. We were unable to remove all of these setae. Later examination of the males after preservation showed that in male #1, six setae remained on the left side, none on the right; in male #2, three setae remained on the left, none on the right, and there were at least five empty sockets; on both males the large setae had been cleanly removed by the first ablation. Male #3 was once again sham operated. Later examination showed it



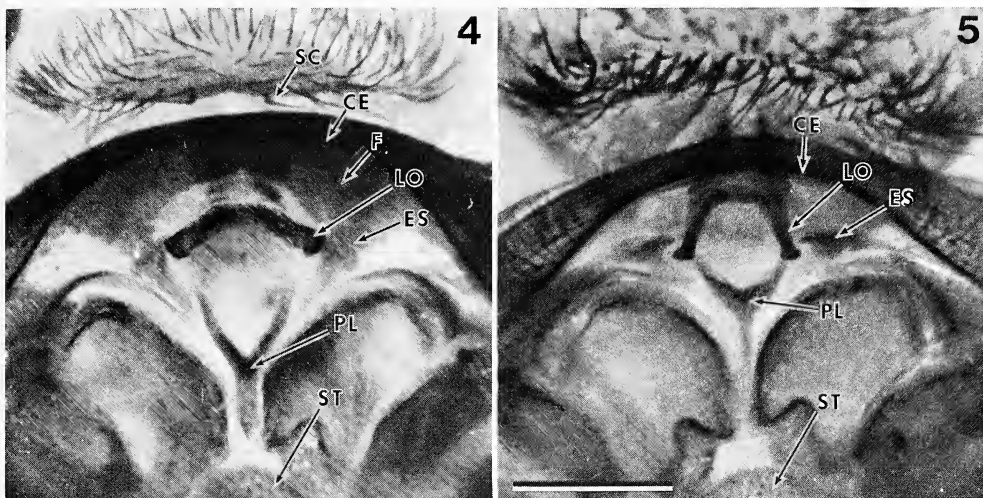
Figs. 2, 3.—*Habronattus cognatus* male: 2, posterior of cephalothorax showing stridulatory file (CE = lower edge of carapace); 3, anterior of abdomen showing two large scraper setae (SC) and several smaller scraper setae (SS). Scale line = 0.1 mm.

had 9 small and 2 large scraper setae. Two hours elapsed between the second operation and the recording. The spiders showed no ill effects from the operations. Sounds were recorded and analyzed as described above.

MORPHOLOGY

Stridulatory apparatus.—An abdomen-carapace stridulatory mechanism, consisting of a file on the back of the cephalothorax and scraper setae on the front of the abdomen, is present in males of all species examined of the *agilis* group (*H. agilis*, *H. alachua*, *H. cognatus*, *H. conjunctus*, *H. elegans*, *H. georgiensis*, *H. peckhami*). Similar mechanisms are known from hahniids, theridiids, gnaphosids and clubionids (Legendre 1963; Uetz and Stratton 1982), and the salticid *Saitis michaelsoni* (Gwynne and Dadour 1985).

The file on the cephalothorax consists of parallel ridges (Fig. 2). The spacing of ridges seems approximately constant from one species to the next, but only two species were measured (from SEMs). The central part of the file has the widest ridge spacing, about 10-11 μm in one male of *H. alachua*. Laterally, the ridges branch and the spacing becomes much narrower, about 4-4.5 μm in *H. cognatus* and 4 μm in *H. alachua*. Females, and males of other groups, lack the file. The file is not part of the carapace proper, but is instead a wide sclerotized portion of the arthrodival membrane just beneath the back of the carapace, as indicated by the carapace-edge ridge lying just above it (Figs. 2, 4 CE) and the attachment of muscle 75 (Fig. 6). The file of *Saitis michaelsoni* is apparently also below the



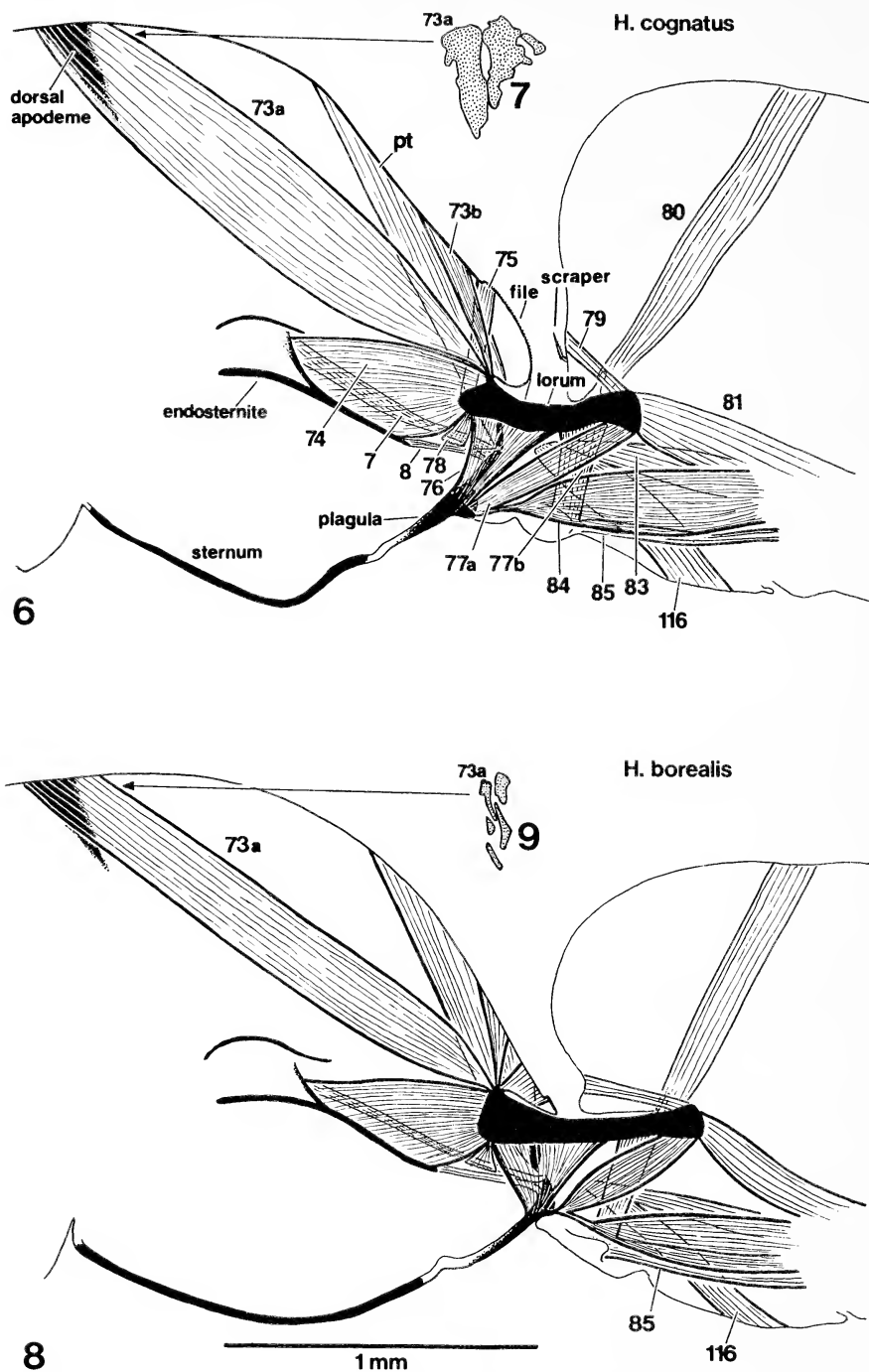
Figs. 4, 5.—Sclerites near pedicel, oblique view from anterior dorsal of cleared integument with most of carapace cut away (CE = carapace edge; F = file viewed from inside; LO = lorum; PL = plagula; SC = scraper seta; ST = sternum); 4, *Habronattus cognatus* male (stridulator; note robust plagula and divergent arms of lorum); 5, *Habronattus calcaratus* male (non-stridulator). Scale line approximately 0.5 mm.

carapace, given Gwynne and Dadour's (1985) SEMs and the captions to their figures b and c on plate I.

The front of the abdomen bears two large curved setae just above the pedicel (Fig. 3 SC) and a series of 4-7 smaller curved setae on each side of the pedicel in males of the *agilis* group (Fig. 3 SS). Both the larger and smaller setae arise and then bend to parallel the surface. The large setae presumably would contact the central coarse part of the file and the smaller setae would contact the lateral fine part of the file. Females of the group have setae similar to, but smaller than, those of males. Males and females of other species groups have no such curved setae.

Sclerites.—Males of the one *agilis*-group species studied, *H. cognatus*, have a number of unusual features of the sclerites near the pedicel. The lorum has anterior arms more robust and divergent than in non-*agilis*-group species studied, *H. calcaratus*, *H. borealis*, *H. americanus*, and *H. decorus* (Figs. 4 and 5, LO). The plagula is much more robust than in *H. borealis* or *H. calcaratus* (Figs. 4 and 5, PL), but only slightly more robust than in *H. decorus* or *H. americanus*. The surface of the abdomen bearing the scraper setae and the epigastric plate are both more heavily sclerotized in males of the *agilis* group than in males of the other *Habronattus* species studied (except *H. americanus*, whose abdominal front is also fairly heavily sclerotized). The sternum of *agilis*-group males is unusually convex (Fig. 6), possibly to accommodate the brain crowded downward by the large lorum-apodeme muscles (see below).

Muscles.—Figures 6-9 show the pedicel musculature of *H. cognatus* (Figs. 6, 7) and *H. borealis* (Figs. 8, 9). Each muscle is labeled with the number of the presumably-homologous muscle in *Latrodectus* (Whitehead and Rempel 1959). Because some muscles differ from those previously reported for spiders, we discuss them briefly here. Whitehead and Rempel report two lorum-carapace muscles in *Latrodectus*, #73 (unpaired) and #75 (paired), while Palmgren (1978)



Figs. 6-9.—Sagittal sections showing musculature of the pedicel region (6, 8), with insets (7, 9) showing exposed carapace attachment surface of dissected muscle 73a: 6, 7, *Habronattus cognatus*; 8, 9, *H. borealis*. Muscle numbering follows Whitehead and Rempel (1959), with exceptions noted in text.

figured only a single lorum-carapace muscle in salticids, his "lt" which he considered homologous to #73 of *Latrodectus*. We found three lorum-carapace muscles, which we call #73a (paired, medially on lorum to dorsal apodeme), #73b (unclear whether paired or unpaired, medially on lorum to back of carapace) and #75 (paired, laterally on lorum to back of carapace). Palmgren's figures suggest that his "lt" is our #73b. Palmgren apparently overlooked #73a, which we have seen in all salticids we have dissected (except *Lyssomanes*), including members of the genera *Acragus*, *Cocalodes*, *Habrocestum*, *Menemerus*, *Phidippus*, *Portia*, *Salticus*, *Sitticus*, and *Talavera*. We have also seen it in an oxyopid (*Oxyopes* sp.). In some of these (*Acragus*, *Cocalodes*, *Menemerus*, *Portia*, and *Oxyopes*) the muscle attaches directly to the dorsal apodeme, while in the others (including *Habronattus*) most or all of the fibers attach to the carapace on either side of the apodeme. Palmgren also did not describe our #75, and he suggested that Whitehead and Rempel's #75 is homologous to his plagulo-tergalis muscle (pt), which it is not. Whitehead and Rempel failed to describe Palmgren's "pt," possibly because they felt that "pt" was just part of the carapace compressor #31, which it may be, for it arises not from the plagula proper but from a small (epimeral?) sclerite closely associated with the lateral arm of the plagula (Figs. 4, 5, ES). Other workers have described only two dorsoventral pedicel compressors (see Brown 1939) whereas we found three, muscles 76, 77a, and 77b. What we label as #77b is a thin sheet and may have been overlooked. Muscles 83, 85 and 116 do not attach to the plagula but to the lateral, ventral and lateral membranous walls, respectively, of the pedicel.

Three musculature differences between *H. cognatus* and *H. borealis* males were notable. The lorum-dorsal apodeme muscle (73a) is not only thicker vertically in *H. cognatus* (Figs. 6, 8), but is much thicker laterally, so that the area of carapace attachment is more than threefold greater (Figs. 7, 9). This difference in thickness was consistent in all specimens examined (nine or more of each species), and is not due just to greater size of *H. cognatus*, for in fact *H. borealis* males are slightly longer and probably more massive. Four other non-*agilis*-group species were also dissected for muscle 73a, and in each the muscle was only about as massive as in *H. borealis*, having a small area of carapace attachment (*H. calcaratus* 1 male, *H. americanus* 2 males, *H. oregonensis* 1 male, *H. decorus* 1 male). The ventral pedicel-abdominal endosternite muscle (85) is thinner in *H. cognatus* than in *H. borealis*, though this does not show well in the illustrations. The lateral pedicel-epigastric plate muscle (116) is considerably broader in *H. cognatus*.

The much greater development of muscles #73a and 116 in *H. cognatus* may be related to the fact that it is a stridulator whereas *H. borealis* and the other four species examined are not (with the possible exception of *H. americanus*; see below). Both *H. cognatus* and *H. borealis* make noise with abdominal motions (see below), but the motion is gentle in *H. borealis*, while in *H. cognatus* the abdomen is vibrated vigorously up and down against the cephalothorax. Muscles #73a and 116 are parallel to the direction of abdominal motion during stridulation, and may supply much of the power for pulling the abdomen up against the carapace. Still, any conclusions about the functional significance of these musculature differences must be viewed as tentative, for the system is partly hydraulic and the effect of a given muscle contraction is difficult to predict.

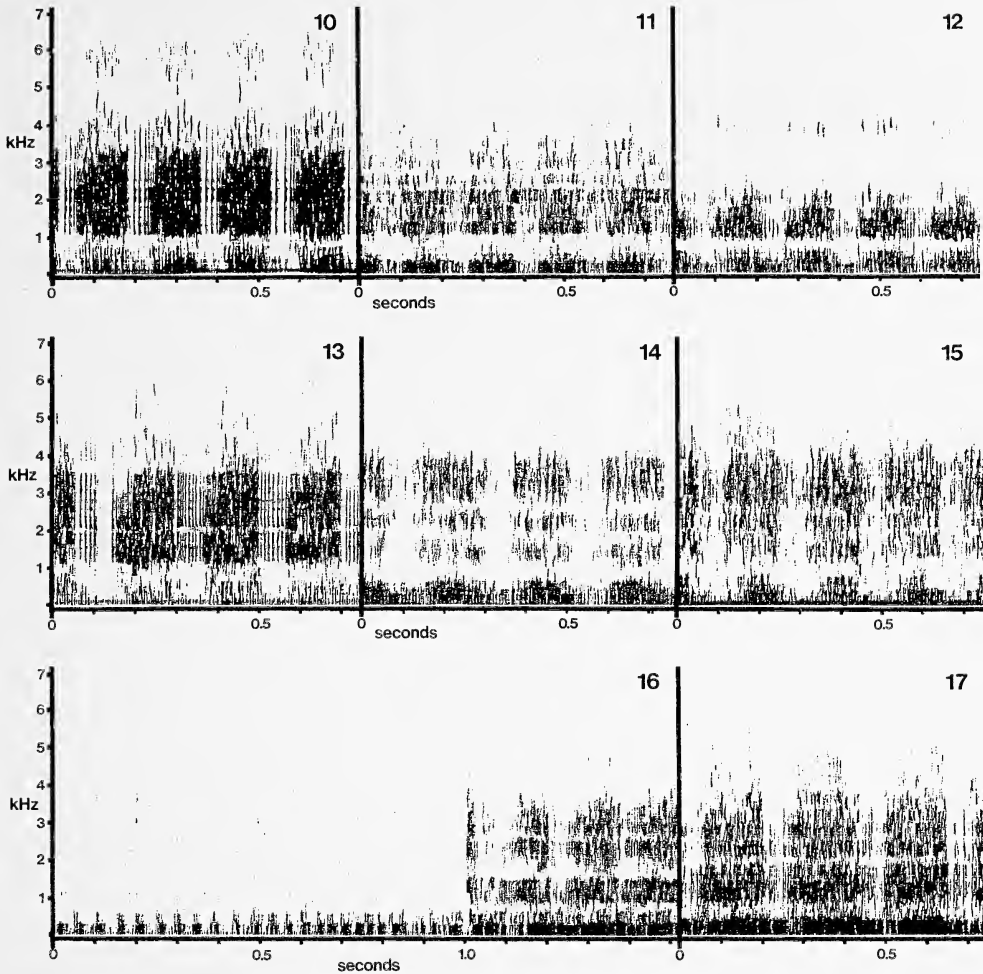
BEHAVIOR AND SOUND

Courtship behavior of male *Habronattus cognatus*.—In the initial stages of courtship three discrete behaviors may be recognized, in each of which some sound is produced. Stationary Abdomen Vibration (SAV) occurs when the male is standing still. The abdomen is raised, such that the ventral surface is parallel to the ground, and is vibrated up and down, striking the back of the cephalothorax in a series of discrete pulses (number of pulses/second = mean 5.5 ± 0.6 SD, range 4.5-6.8, $n = 8$ bouts of SAV by male #1; duration of each pulse 0.12-0.15 second). Sonagram analyses of the sound produced were made for three males. The most prominent sound component is composed of frequencies from about 1 kHz to 3.5 kHz (Figs. 10, 13; the male of Figs. 16, 17 showed a different pattern). There is also a component along the baseline of the sonagram, below 500 Hz. Occasionally a weaker component at 5-6 kHz appears on the sonagrams (Fig. 13). Our recordings showed no component of sound between 8 kHz and 16 kHz (above the range shown in the figures). Between each pulse the sonagrams show a series of vertical lines of 1-3.5 kHz, each line possibly the result of a single stroke of the abdomen (Figs. 10, 13). The sounds produced during SAV are much fainter than those of *Saitis michaelseni*, which are audible from 3-5 m (Gwynne and Dadour 1985). The mean duration of a bout of SAV was 6.0 seconds (± 4.3 SD, range 1.8-14.5, $n = 8$ bouts by male #1).

Abdomen Bobbing (AB) also occurs while the male is standing still, and alternates with SAV. The abdomen is lowered (but not so as to touch the ground), and twitched slightly down and up every 0.3-0.6 seconds, each twitch producing a sound pulse below 500 Hz (Fig. 16). The series of sound pulses resembles the purring of a cat. The mean duration of a bout of AB was 5.4 seconds (± 3.4 SD, range 1.1-12.4, $n = 8$ bouts by male #1).

The Leg Curl display (LC) includes pulsed abdomen vibration like SAV but has in addition vigorous leg and body movements. Typically the male will hold the first pair of legs to the side with the femur either horizontal or slightly above horizontal and the more distal segments curled downward and inward (Fig. 1). With the legs so held, the male sidles quickly and flicks the first pair of legs and palps outward, apparently in synchrony with the pulses of abdomen vibration. The pulses of abdomen vibration occur at higher frequency than during SAV (about 8 pulses/second). The sound produced during LC was much like that produced during SAV, but the sonagram was more irregular, probably because of noise made by the first legs. The mean duration of a bout of LC was 2.4 seconds (± 1.7 SD, range 1.0-8.9, $n = 8$ bouts by male #1). LC is often preceded by SAV, and immediately after LC the male may return to SAV and AB with the legs remaining in the curled position. Though the LC display resembles the hunched-leg agonistic display used by various salticids (e.g., Jackson 1978, 1986a, 1986b), the LC display we observed is no doubt a courtship display given the consistent use of LC by males toward females (seen in all of the approximately 100 bouts of male to female display observed in five species of the *agilis* group), the vigor of its motions, and the failure of males to open the fangs during it.

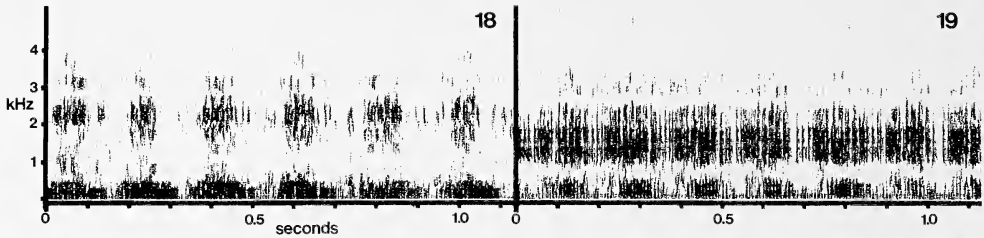
The later stages of courtship have been seen only a few times in *H. cognatus*, and videotaped only once. The male approaches with the first pair of legs held outstretched and forward, sometimes flickering them up and down (Leg Flickering, LF). The male reaches and touches the female on her front femur with



Figs. 10-17.—Sonograms from *Habronattus cognatus* courtship, all from Stationary Abdomen Vibration (SAV) except the first part of 16, which is from Abdomen Bobbing (AB): 10-12, Male #1, 10 before ablation operations; 11, after first ablation operation; 12, after second ablation operation; 13-15, male #2; 13, before ablation operations; 14, after first ablation operation; 15, after second ablation operation; 16-17, male #3; 16, before sham operation (AB until 1.0 second, SAV after 1.0 second); 17, after sham operation.

his first pair of legs before mounting. Our equipment detected no sounds during these later stages save the footsteps of the male.

Courtship behavior of other *agilis*-group members.—We have observed courtship behavior in five other *agilis*-group species. Two species, *H. conjunctus* and *H. elegans*, were videotaped and their sounds recorded. *H. elegans* (three males) display was much like that of *H. cognatus*, with SAV and AB alternating with LC. The frequency of pulses of abdominal vibration during SAV was 4.8-5.5 pulses/second ($n = 2$ bouts for one male from Chilao Campground). Each pulse of sound had one prominent component below 500 Hz, and another component (prominent though not as in *H. cognatus*) at 1.5 to 3 kHz (Fig. 18). The sonogram is different than those for *H. cognatus*, but given the variation observed in *H. cognatus* (Figs. 10, 16) the difference may not be consistent. *H.*



Figs. 18-19.—Sonograms from Stationary Abdomen Vibration of *Habronattus elegans* (18) and *H. conjunctus* (19) courtship.

conjunctus (three males) likewise had a very similar SAV, AB, and LC. The frequency of pulses of abdominal vibration during SAV was 6.3 pulses/second ($n = 1$ for one male from Imperial Co., California). Each pulse had one prominent component below 500 Hz, and another at 1-2.5 kHz (Fig. 19). However, this species only infrequently performed SAV, AB and LC, instead spending more time in the later LF stage and often reaching and touching the female. In the LF stage the legs were sometimes held apart, sometimes forward, but never curled inward. They were flicked up and down in a jerky fashion as the male proceeded more or less straight toward the female. Just before attempting mounting, the male touched the female's femora, as in *H. cognatus*. No sound was heard during LF or later stages. Richman (1982a) described courtship for this species (under the name *Pellenes arizonensis*). He apparently saw both LC ("courtship...often began with the male positioning his front legs in a wide-spread stance, than [sic] moving in a zigzag, crab-like fashion toward the female") and LF ("the front legs were extended and waved a few times"), and the premount femur touch, but no comment is given on sound or the relative frequency of the early and late stages.

We previously observed three *agilis*-group species, *H. agilis* (one male), *H. alachua* (one male) and *H. peckhami* (one male), without videotaping. In all the leg curl display appeared as in *H. cognatus*, with the first legs curled and flicking while the male sidles and vibrates the abdomen. The pulsed rasping noise produced by the abdomen was heard, but not recorded, in *H. agilis* and *H. peckhami*. Later stages in LF and premount femoral touching were also observed once in *H. agilis*. Emerton (1909: 230) describes and figures what is apparently LF in *H. agilis*. Richman (1982b) gives a brief description of the display of another *agilis*-group species, *H. georgiensis* (under the name *Pellenes agilis*), indicating that the abdomen is twitched up and down.

These observations indicate much uniformity of courtship, at least to a human's eyes and ears, throughout the species group. Except for the greater frequency of LF in *H. conjunctus*, we detected no significant differences in courtship of these species, all showing LC, and those studied closely showing SAV and AB. If these taxa are indeed all reproductively isolated, females may discriminate by color patterns on the face and first legs, which differ markedly among the species.

Courtship behavior of other *Habronattus*.—For purposes of comparison, the courtship of three *Habronattus* species in different species groups were also videotaped: *H. borealis*, *H. americanus* and *H. oregonensis*. In none of these species is there an obvious file and scraper mechanism on the carapace and abdomen, and yet in two of these species abdominal movements produces an easily recorded sound.

In *H. borealis* courtship the first legs are raised and held forward as the male sidles and waves his palps over his front femora. The male then moves the palps forward and stops walking, flicks the first legs' tips a few times, then alternately shuffles the left and right third legs, then waves the first legs inwards a few times, then waves the first legs rapidly as he proceeds to mount. In the second last stage, each time the legs are waved inward the abdomen is depressed and a faint buzz can be heard. The abdomen does not contact the substrate, nor does it rub against the carapace.

In *H. americanus* the male sidles with first legs bowed and held forward and the palps down and apart. When close he suddenly stands high, reaches forward and rapidly pulls the first legs down and in against the substratum and/or the back of the female's first pair of legs, as he simultaneously lowers the front of his abdomen down against the back of his carapace. Relatively loud sounds are produced by this, possibly with contributions from both the first legs and the abdomen. While *H. americanus* males have an unmodified carapace and lack scraper setae, the front of the abdomen is heavily sclerotized and rugose, and stridulation may be occurring.

In *H. oregonensis* the male holds the first legs to the side (see figure on p. 359 of Peckham and Peckham 1909) and waves them slightly as he sidles. When close to the female he holds the first legs forward and vibrates one or the other. Our recordings showed no sounds nor were abdominal vibrations seen.

ABLATION EXPERIMENTS

Thus far we have described a scraper and file, and the abdominal movements and sounds produced, but the question remains: are the sounds heard during courtship of the *agilis* group due solely to the rubbing of the scraper setae against the file? Our ablation experiments indicate that the scraper setae do indeed contribute sound, but that these may not be the only sources of sound. The results are preliminary, for we performed incomplete ablation experiments on only two males. Also, the substrate-borne component of the sound, which we did not directly measure, may be important to the spider.

After the first ablation of the large scraper setae, the sound produced by abdominal vibration during SAV was diminished and changed in quality, both to our ears and according to the sonagrams. The prominent 1-3.5 kHz component was lessened in both males #1 and #2, but the component below 500 Hz seemed unaffected (Figs. 11, 14). Frequencies of 2.5-3.5 kHz were especially diminished in male #1, whereas in male #2 the 1-2.5 kHz sounds were diminished. Because of the different responses of the two males, the exact frequencies contributed by the scraper setae is uncertain. The vertical lines between pulses were no longer clear on the sonagrams after ablation, suggesting that they may be made by the large scraper setae; however, these lines also seemed absent from the recordings of male #3 whose setae were intact. The second ablation produced little change from the first (Figs. 12, 15), although the sounds appeared to have diminished further. The drop in absolute sound intensities is not accurately known, because recorded intensity depended on the spider's exact position on the cardboard. Still, to our ears the sound after both operations seemed to be at least half as loud as the pre-operation sound. Neither ablation affected (to our ears) the purring sound from

AB, as expected since the abdomen does not contact the cephalothorax during AB. Male #3's sound was essentially unchanged following its sham operation (Fig. 17).

Given that ablation of 1/2 to 3/4 of the setae decreased the sound but not proportionately, it appears that sound below 500 Hz and perhaps some between 1 and 3.5 kHz is produced without the aid of these setae. How then is it produced? The common salticid courtship behavior of twitching the abdomen down and up (Jackson 1982) actually produces a low frequency sound (at or below 500 Hz), even though the twitch of the abdomen seems slight and there is no carapace or substratum contact (Maddison and Stratton 1988); the sound may be produced by the legs recoiling against the substrate with each abdominal twitch. *Habronattus cognatus* also performs this abdomen twitching behavior: we have called it "AB" and the sound produced "purring". If such subtle motion of the abdomen can make audible sound, then the vigorous abdomen vibration during SAV may produce much of its sound by the same mechanism, and the scraper setae merely add a component, albeit a strong one, by stridulation. This is consistent with the observation that frequencies below 500 Hz were relatively untouched by ablation (Figs. 11, 12, 14, 15).

The communicatory significance of the abdominal vibration during courtship needs to be determined, although it is difficult to use females of these species for behavioral assays, for they rarely accept males in the laboratory. It would also be necessary to determine the relative importance of air- versus substrate-borne vibrations. Further research should examine these parameters.

Another topic for future research is the possible use of stridulation in other contexts by these species, such as during threat display of male-male interactions. We have observed male-male interactions in *Habronattus cognatus* only once; the first legs were held curled as in LC, the carapace was raised and the abdomen bent down toward the substrate. The first legs and palpi were stationary during the display. The depressed position of the abdomen might suggest that stridulation could not be accomplished, but given our limited observations we must allow for the possibility that stridulation might generally be a part of male-male threat display.

Perhaps the abdomen vibration and stridulation in the *agilis* group and in *Saitis michaelseni* have evolved as extreme forms of the abdominal twitching common in salticids (Gwynne and Dadour 1985). If so, then both the *agilis* group and *S. michaelseni* have enhanced the sound from twitching with very similar stridulatory mechanisms. Other salticids may have taken other routes to enhancing the sound. A number of euophryines in both the New World (species placed in *Cobanus*, *Agobardus*, *Antillattus*, *Siloca*) and Old World (*Stagetilus*, *Eustirognathus*) have the integument just anterior to the tracheal spiracle sclerotized and swollen into a bump (see Bryant 1943, Fig. 91). Behavioral observations need to be made on these genera to test whether the bump might be used percussively against the substrate.

A broader survey of species is clearly needed to reveal the patterns and diversity in the evolution of noisemaking in salticids. While stridulatory mechanisms such as that found in the *Habronattus agilis* group may be rare in salticids, many species make noises (Maddison and Stratton 1988). The importance of acoustic communication to salticids has probably been underestimated.

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GROUND SURFACE SPIDERS IN THREE CENTRAL FLORIDA PLANT COMMUNITIES

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ABSTRACT

Ground surface spiders were pitfall-trapped every two months in pond pine, sand pine scrub, and flatwoods plant communities on the University of Central Florida campus near Orlando from May, 1983 to March, 1984. Eight-two species and 2,326 individuals were collected: 57 species and 1,094 individuals in pond pine, 42 species and 851 individuals in sand pine scrub, and 48 species and 381 individuals in flatwoods community.

Spider diversity was greatest in pond pine, followed by sand pine scrub, and then flatwoods community. Similarity in spider species was greatest between pond pine and flatwoods, followed by sand pine scrub and flatwoods, and then pond pine and sand pine scrub.

A new species of *Drassyllus* (Gnaphosidae) was collected in the flatwoods and a range extension for *Zora pumila* (Zoridae) was recorded in pond pine.

INTRODUCTION

Spider populations in different plant communities have been studied by Lowrie (1942, 1968, 1985), Duffey (1962), Berry (1970, 1971), Barnes (1953), Uetz (1975, 1977, 1979), Bultman et al. (1982), and many other investigators. The spider faunas associated with plant communities in Florida are poorly defined, although important studies have been done by Muma (1973), Rey and McCoy (1983), and Lowrie (1963, 1971). Muma (1973) compared ground surface spider population in four central Florida ecosystems. Rey and McCoy (1983) sampled arthropods including spiders of northwest Florida salt marshes. Lowrie, working in the Pensacola area of northwest Florida, studied effects of grazing and intense collecting on a population of green lynx spiders (1963) and the effects of time of day and weather on spider catches with sweep nets (1971).

Our primary purposes were to determine and compare the ground surface spider fauna in pond pine, sand pine scrub, and flatwoods communities. In addition, we wanted to determine if seasonal differences exist in the spider populations among the three plant communities.

STUDY AREA

The three plant communities were in the eastern part of the University of Central Florida campus, located approximately 17 km east of Orlando in Orange County. Plant names mentioned herein are according to Wunderlin (1982).

Plant cover in the pond pine community consisted of shrubs, trees, tree seedlings, grasses, and vines. A large accumulation of leaf litter was present. Pond pine (*Pinus serotina* Michx.) was the dominant tree followed by two bays (*Gordonia lasianthus* (L.) Ellis and *Magnolia virginica* L., dahoon holly (*Ilex cassine* L.), and swamp black gum (*Nyssa sylvatica* Marsh.). Saw palmetto (*Serenoa repens* (Bartr.) Small) was common. Soil in pond pine was rutledge fine sand, a highly acidic type with low organic matter.

Ground surface in the sand pine scrub community was covered with a sparse leaf litter. The soil type was St. Lucie fine sand, which is low in organic matter, very acidic, nutrient deficient, and with low water-holding capacity. Dominant shrubs were myrtle oak (*Quercus myrtifolia* Willd.) and rusty lyonia (*Lyonia ferruginea* (Walt.) Nutt.). Sand pine (*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.) was the dominant tree, but scrub live oak (*Q. geminata* Small), Chapman's oak (*Q. chapmanii* Sarg.), and saw palmetto were common.

The flatwoods site contained Leon fine sand, which is very acidic, low in organic matter, and poorly drained. Plants were mainly saw palmetto, longleaf pine (*P. palustris* Mill.), and two wiregrasses, *Aristida spiciformis* Ell. and *A. stricta* Michx. Ground cover consisted mainly of saw palmettos and grasses. See Corey (1987) for a more detailed description of the plants in each community.

MATERIALS AND METHODS

The three communities were sampled every two months starting in May, 1983 and ending in March, 1984. Ninety pitfall traps were deployed. (See Corey (1987) and Corey and Taylor (1987) for pitfall trap design). Ten traps each were placed in three sites in each plant community (pond pine: sites A, B, and C; sand pine scrub: sites D, E, and F; and flatwoods: sites G, H, and I). Pitfall traps were placed in a line transect with each trap at least 10 m apart. Trap lines were 20-50m apart. Each trap contained a 0.47-liter mixture of ethylene glycol, 95% ethanol, and water in a ratio of 2:1:2.

Thirty collections per plant community were made each collection month for a total of 540 pitfall collections. During each collection month, the pitfall traps remained open for 14 days. After that time, the contents of each trap was separated from the fluid using a fine-mesh wire screen and emptied into a baby food jar containing 70% ethanol. After each trap collection, the fluid was filtered, reconstituted back to its original volume, and reused.

Spiders were identified using a dissecting microscope. Difficult specimens were verified or identified by Jonathan Reiskind, University of Florida; Jonathan Coddington, Smithsonian Institution; Norman I. Platnick, American Museum of Natural History; J. H. Redner, Biosystematics Research Institute; and G. B. Edwards, Florida Department of Agriculture and Consumer Services.

Many immature spiders were identified to family. Some spiders were collected in poor condition and could not be identified to family; these specimens are reported as undetermined (See Table 3).

RESULTS AND DISCUSSION

A total of 2,326 spiders representing 82 species in 22 families, was captured in 540 pitfall trap collections. An overall average of 4.31 spiders was observed per

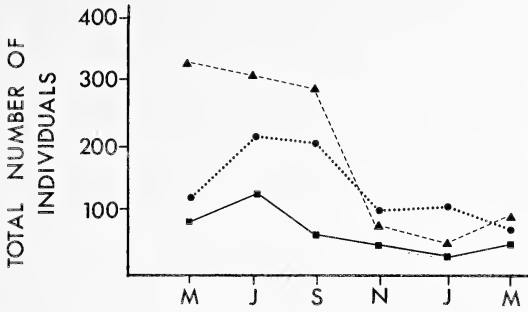


Fig. 1.—Total number of spiders caught on the ground surface using pitfall traps in pond pine (▲), sand pine scrub (●), and flatwoods (■).

pitfall trap. Forty-seven percent of the combined spider assemblage for the three communities was captured in pond pine, 36.6% in sand pine scrub, and 16.4% in flatwoods. More spiders were trapped in July than in any other month, except for pond pine where the greatest number occurred in May (Fig. 1). Few spiders were collected in November and January.

Pond pine yielded 1,094 individuals, 57 species, and 21 families; sand pine scrub, 851 individuals, 42 species, and 13 families; flatwoods, 381 individuals, 48 species, and 17 families. Sixty-five percent more spiders were found in pond pine than in flatwoods, 22% more in pond pine than in sand pine scrub, and 55% more in sand pine scrub than in flatwoods. A species list of all spiders collected appears separately (Corey 1987).

Most spiders were captured during summer months; similar results have been reported by Turnbull (1960), Berry (1971), and Uetz (1975).

The greater spider abundance and species richness found in pond pine, compared to scrub and flatwoods communities, may be correlated with its dense litter and generally moist ground surface. Litter and soil moisture have been shown to be correlated with spider species richness, abundance, and diversity by Uetz (1975, 1977, 1979), Bultman and Uetz (1982), Cady (1984), and Lowrie (1948, 1968). In contrast, flatwoods periodically had standing water after hard rains, but lacked a dense leaf litter to retain moisture; sand pine scrub was dry throughout the study.

Analysis of guild composition shows differences between communities (Fig. 2). Guilds were patterned after Bultman et al. (1982). Several families not represented

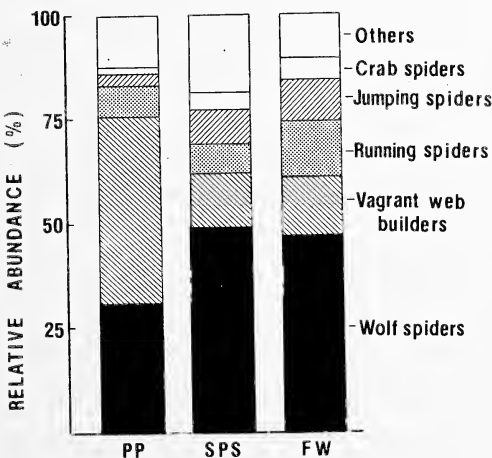


Fig. 2.—Guild composition of spider communities from the three study sites. PP = pond pine, SPS = sand pine scrub, and FW = flatwoods.

Table 1.—Mean number of individuals occurring in the study sites on the ground surface.

| Collection Month | COMMUNITY | | |
|---------------------|---------------------------------|---------------------------------------|---------------------------------|
| | POND PINE $\bar{x} \pm (SE)$ | SAND PINE SCRUB $\bar{x} \pm (SE)$ | FLATWOODS $\bar{x} \pm (SE)$ |
| May | 104.67 (9.22) | 40.67 (3.85) | 31.00 (6.66) |
| July | 102.00 (16.52) | 75.67 (5.21) | 40.67 (14.42) |
| September | 81.33 (3.18) | 67.67 (0.34) | 17.33 (4.67) |
| November | 22.00 (2.09) | 35.00 (7.10) | 14.00 (1.53) |
| January | 17.33 (3.94) | 40.33 (4.67) | 8.67 (1.86) |
| March | 34.00 (6.66) | 24.33 (5.05) | 15.67 (0.33) |

in the Bultman et al. study were placed in a guild based on Gertsch (1979). Guilds are (1) wolf spiders, Lycosidae; (2) vagrant web builders, Agelenidae and Hahniidae; (3) running spiders, Ctenidae, Gnaphosidae, and Clubionidae; (4) jumping spiders, Salticidae; (5) crab spiders, Thomisidae and Sparassidae; and (6) others; remainder of the spider families. Relative abundance of wolf spiders declined in pond pine from sand pine scrub and flatwoods. This may be due to the large amount of leaf litter in pond pine. Similar results were reported by Bultman et al. (1982) and Lowrie (1948). Vagrant web builders increased substantively in pond pine. These spiders live within the litter and have been found to increase in abundance with greater amount of litter (Bultman et al. 1982; Uetz 1979). The changes in the vagrant web builders are due to a single species, *Hahnina cinerea* Emerton. Bultman et al. also found a single species, *Neoantistea magna* (Keys.), to be responsible for an increase in vagrant web builders in a beech-maple community.

Sorensen's Index of Similarity (Krebs 1978) was used to determine the similarities of spider species composition among communities. Species composition was more similar between pond pine and flatwoods (0.65), followed by sand pine scrub and flatwoods (0.56). Pond pine and sand pine scrub (0.51) were least similar.

Table 1 shows the mean number of individuals occurring in the three communities. For each monthly mean 95% confidence intervals were calculated as $\bar{x} \pm t_2 (SE)$ (Simpson et al. 1960). Pond pine in May was significantly different from the other communities in mean number of individuals; in September flatwoods was different from the other communities. Mean number of individuals captured in flatwoods in January were significantly different from sand pine scrub, but not pond pine. In contrast, no significant differences ($p > 0.05$) were

Table 2.—Mean number of species occurring in the study sites on the ground surface.

| Collection Month | COMMUNITY | | |
|---------------------|---------------------------------|---------------------------------------|---------------------------------|
| | POND PINE $\bar{x} \pm (SE)$ | SAND PINE SCRUB $\bar{x} \pm (SE)$ | FLATWOODS $\bar{x} \pm (SE)$ |
| May | 15.00 (1.16) | 9.33 (1.34) | 15.67 (2.03) |
| July | 13.67 (0.88) | 14.33 (0.66) | 10.00 (1.00) |
| September | 10.67 (1.20) | 12.67 (0.34) | 8.00 (2.09) |
| November | 8.00 (0.00) | 8.00 (2.00) | 7.00 (2.00) |
| January | 4.33 (0.66) | 7.33 (1.34) | 4.33 (0.88) |
| March | 10.33 (0.34) | 10.33 (1.46) | 9.67 (1.20) |

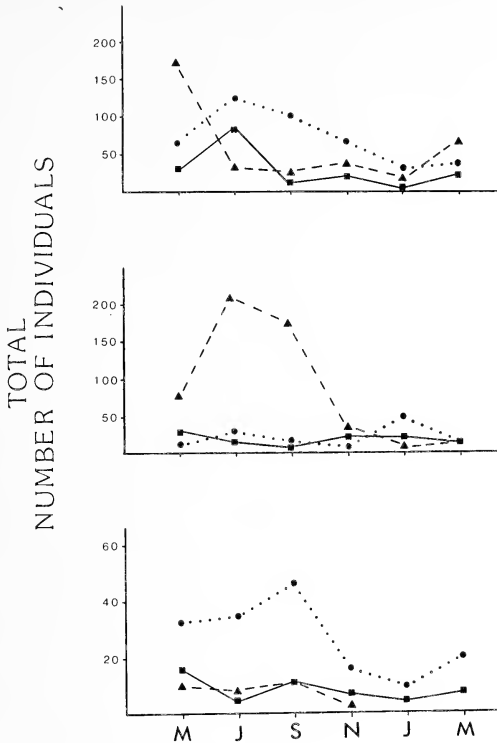


Fig. 3.—Seasonal distribution of the most common families of ground surface spiders caught in pitfall traps in pond pine (▲), sand pine scrub (●), and flatwoods (■). Lycosidae (upper), Hahniidae (middle), and Salticidae (lower).

found between the mean number of species occurring in the three communities during the collecting months (Table 2). This result may be due to the large variance in number of species found among the communities.

Species diversity, based on Simpson's Index of Diversity (Simpson 1949), was low for all communities. Pond pine had a value of 0.71, sand pine scrub of 0.90, and flatwoods of 0.94. This might be due to the high species richness and small number of dominant species found.

Spider families, represented by individuals collected on the ground surface, are listed in Table 3. Over all communities, the three most common families were lycosids, hahniids, salticids; collectively, they represent 72.5% of all spiders captured in pitfall traps. In pond pine, hahniids, lycosids, and ctenids represented 79.5% of that community's total spider assemblage. In sand pine scrub, lycosids, salticids, and hahniids represented 80.3% of the total spider assemblage. In flatwoods, lycosids, hahniids, and salticids represented 70.6% of the total spider assemblage. Figure 3 shows seasonal abundance of three common families occurring on the ground surface.

The species composition in our study differed from that found by Muma (1973) who studied ground surface spiders in sand pine dune and pine flatwoods near Winter Haven, Florida. Only seven species were common to his sand pine dune and our sand pine scrub habitats. These were *Pholcomma hirsuta* Emerton, *Hahnina cinerea*, *Trochosa parthenus* Simon, *Sosippus floridanus* Simon, *Cesonia bilineata* (Hentz), *Drassyllus seminolus* (Chamb. & Gertsch), and *Castianeira floridana* (Banks). In pine flatwoods, only *Neoantista agilis* (Keys.), *Sosippus floridanus*, and *Oxyopes salticus* (Hentz) were found in both studies. Reasons for the small number of spider species common to both studies are unknown.

Table 3.—Number of individuals collected and percent of spiders by family for the three communities.

| FAMILY | POND PINE | | SAND PINE | | FLATWOODS | | TOTAL | |
|-------------------|-----------|------|-----------|------|-----------|------|-------|------|
| | # | % | # | % | # | % | # | % |
| Oecobiidae | 3 | 0.3 | 0 | 0.0 | 1 | 0.3 | 4 | 0.2 |
| Uloboridae | 3 | 0.3 | 0 | 0.0 | 3 | 0.8 | 6 | 0.3 |
| Dictynidae | 2 | 0.2 | 0 | 0.0 | 0 | 0.0 | 2 | 0.1 |
| Oonopidae | 6 | 0.6 | 0 | 0.0 | 1 | 0.3 | 7 | 0.3 |
| Pholcidae | 2 | 0.2 | 0 | 0.0 | 1 | 0.3 | 3 | 0.1 |
| Theridiidae | 18 | 1.6 | 12 | 1.4 | 13 | 3.4 | 43 | 1.8 |
| Mymenidae | 1 | 0.1 | 0 | 0.0 | 0 | 0.0 | 1 | 0.04 |
| Linyphiidae | 21 | 1.9 | 29 | 3.4 | 11 | 2.8 | 61 | 2.6 |
| Linyphiinae | 2 | 0.2 | 2 | 0.2 | 3 | 0.8 | 7 | 0.3 |
| Erigoninae | 19 | 1.7 | 26 | 3.1 | 8 | 2.1 | 53 | 2.3 |
| Araneidae | 1 | 0.1 | 1 | 0.1 | 0 | 0.0 | 2 | 0.1 |
| Theridiosomatidae | 5 | 0.5 | 0 | 0.0 | 0 | 0.0 | 5 | 0.1 |
| Tetragnathidae | 1 | 0.1 | 1 | 0.1 | 1 | 0.3 | 3 | 0.1 |
| Agelenidae | 2 | 0.2 | 4 | 0.5 | 1 | 0.3 | 7 | 0.3 |
| Hahniidae | 481 | 44.0 | 106 | 12.5 | 52 | 13.7 | 639 | 27.4 |
| Lycosidae | 344 | 31.4 | 424 | 49.8 | 180 | 47.2 | 948 | 40.8 |
| Oxyopidae | 7 | 0.6 | 4 | 0.5 | 2 | 0.5 | 13 | 0.6 |
| Gnaphosidae | 12 | 1.1 | 24 | 2.8 | 28 | 7.4 | 64 | 2.8 |
| Clubionidae | 26 | 2.4 | 16 | 1.9 | 14 | 3.7 | 56 | 2.4 |
| Zoridae | 1 | 0.1 | 0 | 0.0 | 0 | 0.0 | 1 | 0.04 |
| Ctenidae | 45 | 4.1 | 18 | 2.1 | 10 | 2.6 | 73 | 3.1 |
| Sparassidae | 0 | 0.0 | 0 | 0.0 | 1 | 0.3 | 1 | 0.04 |
| Thomisidae | 16 | 1.5 | 34 | 4.0 | 18 | 4.7 | 68 | 2.9 |
| Salticidae | 27 | 2.5 | 153 | 18.0 | 35 | 9.7 | 215 | 9.3 |
| Undetermined | 70 | 6.4 | 25 | 2.9 | 9 | 2.4 | 104 | 4.5 |

Our study and that of Muma's (1973) show important differences in species compositions of spiders between communities. In our sand pine sites, lycosids, salticids, and hahniids comprised 80.3% of the spider population. In contrast, lycosids (53%), gnaphosids (19%), and salticids (18%) totaled 90% of the spider population in the sand pine dune studied by Muma (1973). In our flatwoods community lycosids, hahniids, and salticids comprised 70.6% of the total spider population, whereas 90% of the total population in Muma's pine flatwoods consisted of lycosids (64%), salticids (21%), and linyphiids (5%). Differences in the two studies may be due to temporal changes in Florida habitats.

Table 4 shows the 15 commonest species collected by frequency of occurrence. The three most common species for all communities were *Hahnina cineria*, *Habrocestum bufoides* Chamberlin & Ivie, and *Pardosa* sp. #1.

Nineteen species occurred in all communities (Table 5). *Hahnina cinerea* was common in all communities and *Sosippus floridanus* and *H. bufoides* were common in sand pine scrub and flatwoods.

Changes in the seasonal cycle were due to variation in the population of each individual species and also to the appearance and disappearance of species at different times of the year. The largest number of adult spiders in all three communities occurred during the summer. Three species had two different months with large population peaks; *Centus captiosus* Gertsch in July and January, *Oxyptila modesta* (Scheffer) in November and March, and *Zelotes pullus* Bryant in September and March. *Hahnina cinerea* was present in large

Table 4.—Fifteen spider species ranked by frequency of occurrence within each plant community.

| SPECIES | POND PINE | SAND PINE SCRUB | FLATWOODS |
|---|--------------|--------------------|-----------|
| <i>Hahnina cinerea</i> Emerton | 1 | 2 | 1 |
| <i>Schizocosa</i> sp. | 2 | — | — |
| <i>Pardosa</i> sp. #2 | 3 | 14 | 9 |
| <i>Ctenus captiosus</i> Gertsch | 4 | 9 | 8 |
| <i>Lycosa punctulata</i> (Hentz) | 5 | — | 10 |
| <i>Lycosa</i> sp. #1 | 6 | 5 | 10 |
| <i>Schizocosa duplex</i> Chamberlin | 7 | 6 | — |
| <i>Oxyptila modesta</i> (Scheffer) | 8 | 7 | 5 |
| <i>Sosippus floridanus</i> Simon | 9 | 4 | 2 |
| <i>Pirata alachuus</i> Gertsch & Wallace | 10 | — | — |
| <i>Habrocestum bufoides</i> Chamberlin & Ivie | 11 | 1 | 3 |
| <i>Zelotes pullus</i> Bryant | 11 | 11 | 6 |
| <i>Thymoites</i> sp. | 11 | — | 12 |
| <i>Corythalia</i> sp. | 11 | — | — |
| <i>Trachelas deceptus</i> (Banks) | 15 | — | — |
| <i>Trochosa partenus</i> Simon | — | 8 | 7 |
| <i>Pardosa</i> sp. #1 | — | 3 | — |
| Erigoninae sp. #3 | — | 10 | — |
| <i>Theridion alabamense</i> Gertsch & Wallace | — | 13 | — |
| <i>Neoantistea agilis</i> (Key.) | — | — | 4 |
| Lycosidae sp. #2 | — | 11 | — |
| Lycosidae sp. #3 | — | 14 | — |
| <i>Castianeira floridana</i> (Banks) | — | 14 | — |
| <i>Drassyllus</i> sp. | — | — | 12 |
| Lycosidae sp. #1 | — | — | 12 |
| <i>Litophyllus temporarius</i> Chamberlin | — | — | 15 |

Table 5.—Spiders found in all three plant communities and their relative abundance (R = rare, less than 1% of the total population for that community; P = present, 1-4.9%; and C = common, 5% or more).

| SPECIES | POND PINE | SAND PINE SCRUB | FLATWOODS |
|---|--------------|--------------------|-----------|
| <i>Pholcomma hirsutum</i> Emerton | R | R | R |
| <i>Theridion alabamense</i> Gertsch & Wallace | R | R | P |
| <i>Thymoites</i> sp. | R | R | R |
| Erigoninae sp. #3 | R | P | R |
| <i>Hahnina cinerea</i> Emerton | C | C | C |
| <i>Schizocosa duplex</i> Chamberlin | R | P | P |
| <i>Schizocosa</i> sp. | C | R | R |
| <i>Sosippus floridanus</i> Simon | P | C | C |
| <i>Pardosa</i> sp. #1 | R | C | P |
| <i>Pardosa</i> sp. #2 | C | R | P |
| <i>Lycosa</i> sp. #1 | P | P | P |
| <i>Zelotes pullus</i> Bryant | R | P | P |
| <i>Litopyllus temporarius</i> Chamberlin | R | R | P |
| <i>Castianeira floridana</i> (Banks) | R | R | R |
| <i>C. longipalpus</i> (Hentz) | R | R | R |
| <i>Ctenus captiosus</i> Gertsch | P | P | P |
| <i>Oxyptila modesta</i> (Scheffer) | P | P | P |
| <i>Habrocestum bufoides</i> Chamberlin & Ivie | R | C | C |
| <i>Metacryba</i> sp. | R | R | R |

numbers from July through September in pond pine and flatwoods, but in January in sand pine scrub. *Ctenus captiosus* appeared in large numbers in summer in pond pine and sand pine scrub, but in the fall in flatwoods.

Berry (1971) found that adults and juveniles of some species appeared in large numbers after a period of time when no or very few adults or juveniles were found. *Sosippus floridanus*, *Trochosa parthenus*, *Zelotes pullus*, and *Habrocestum bufoides* exhibited this behavior in our study. These species were found in small numbers in November through March and in large numbers beginning in May. These species may overwinter as juveniles or eggs.

A new species of *Drassyllus* was found in flatwoods (Platnick, pres. comm.). Four males and one female were caught in May at sites G (three individuals) and I (two individuals). One female *Zora pumila* (Hentz) was found in May at site B of the pond pine community; the previous southernmost limit of its range was Alabama (Kaston 1978).

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ARBOREAL SPIDERS (ARANEAE) ON BALSAM FIR AND SPRUCES IN EAST-CENTRAL MAINE

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ABSTRACT

Spiders of 11 families, 22 genera, and at least 33 species were collected from crown foliage samples of *Abies balsamea* (L.) Mill., *Picea rubens* Sarg., and *Picea glauca* (Moench) Voss in east-central Maine. For both study years (1985, 1986), spider species composition varied by foraging strategy (web spinner, hunter) and among 10 study sites. Numbers, life stages, and sex ratios of spiders also differed between study years. Spider densities per m² of foliage area generally were greater ($P \leq 0.05$) on spruces ($\bar{X} = 16.3 \pm 1.1$) than on fir ($\bar{X} = 10.9 \pm 1.0$). Estimates of absolute populations of arboreal spiders ranged from 35,139 to 323,080/ha; of spruce budworm from 271,401 to 6,122,919/ha. Spider-budworm densities/ha covaried significantly ($P \leq 0.001$) each year ($r = 0.84$, 1985; $r = 0.71$, 1986). None of the measured forest-stand parameters (basal area, tree species percentage) were reliable predictors of spider populations/ha.

INTRODUCTION

Recent devastating outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.), have renewed interest in determining potential natural enemies of this defoliator of northeastern spruce-fir forests. Because of their ubiquitous occurrence, relative abundance, and predatory habits, spiders are considered important predators of the spruce budworm (Morris 1963; Jennings and Crawford 1985). Watt (1963) estimated that only 0.49 larvae/m² of tree foliage would have to be eaten by predators, including spiders, to account for a decrease in population survival rate of the spruce budworm.

A necessary first step for determining potential natural enemies of any pest is identification of the associated fauna. Some information is available about spiders of northeastern spruce-fir forests; however, most studies concern the terricolous fauna (Freitag et al. 1969; Carter and Brown 1973; Varty and Carter 1974; Jennings et al. 1988; Hilburn and Jennings 1988). Few previous studies have dealt with the arboreal spiders found on foliage of spruces (*Picea* spp.) and firs (*Abies* spp.); only one study (Jennings and Collins 1987) was completed in Maine.

During recent investigations of microsporidia-infected budworms, arboreal spider and spruce budworm populations were assessed on balsam fir, *Abies balsamea* (L.) Mill., red spruce, *Picea rubens* Sarg., and white spruce, *Picea glauca* (Moench) Voss trees in east-central Maine. This paper describes the arboreal-spider fauna associated with these coniferous tree species, compares spider-spruce budworm population densities among study sites and between host-tree species, estimates absolute population densities of spiders and budworms per hectare, and explores possible relationships among spiders, budworms, and forest-stand parameters.

METHODS

Study areas.—Six forest stands were investigated in 1985; four were investigated in 1986. All study sites were in east-central Maine (Fig. 1), and were in open, fir-spruce stands that had moderate to heavy infestations of spruce budworm. Site locations, abbreviations, and sampling years were:

- Big Lake (BL)-T27 ED, Washington County; 1985.
- Deer Lake (DL-'85)-T34 MD, east, Hancock County; 1985.
- Deer Lake (DL-'86)-T34 MD, south, Hancock County; 1986.
- Eastern Road (ER)-Upper Molunkus Twp., Aroostook County; 1985.
- Machias River (MR)-T31 MD, Washington County; 1986.
- Myra (MY-'85)-T32 MD, Hancock County; 1985.
- Myra (MY-'86)-T32 MD, east, Hancock County; 1986.
- Old Stream (OS)-T31 MD, Washington County; 1986.
- Raven (RA)-Macwahoc Plt., Aroostook County; 1985.
- River Road (RR)-Mattawamkeag Twp., Penobscot County; 1985.

At each study location, linear transects (0.5 to 1 km) were established along old logging roads or forest trails. We used a variable-size plot design to facilitate tree selection. Branch samples were obtained with a long, extendable pole pruner. Ten or 20 dominant/codominant trees of each category (balsam fir-red spruce; balsam fir-white spruce; balsam fir) were selected, flagged, and numbered for consecutive sampling on a weekly basis.

Stand measurements.—The variable-plot sample method (Wenger 1984) was used to determine basal areas (m^2/ha) of balsam fir, spruces (both red and white), northern white-cedar, *Thuja occidentalis* L., eastern white pine, *Pinus strobus* L., eastern hemlock, *Tsuga canadensis* (L.) Carr., and hardwoods (mostly *Acer* spp. and *Betula* spp.). At each study site (except DL-'85), ten 10-factor prism plots were established and all trees ≥ 2.54 cm tallied by species or species group (e.g., spruces, hardwoods). Only four prism plots were taken at DL-'85.

Branch samples.—Trees were sampled at about weekly intervals both study years. In 1985, sampling began 20 May and ended 12 July; in 1986, sampling began 10 June and ended 2 July. Each year, the duration of the sampling period corresponded with the early larval (L_3 - L_4) through pupal stages of the spruce budworm. This allowed determination of predator-prey densities when budworm larvae and pupae are susceptible to predation (Morris 1963).

At each sampling, one 45-cm branch was pruned from the upper crown half of each sample tree. Sectional, aluminum pole pruners equipped with a cloth-basket attachment below the pruner head were used to cut and lower branches to the

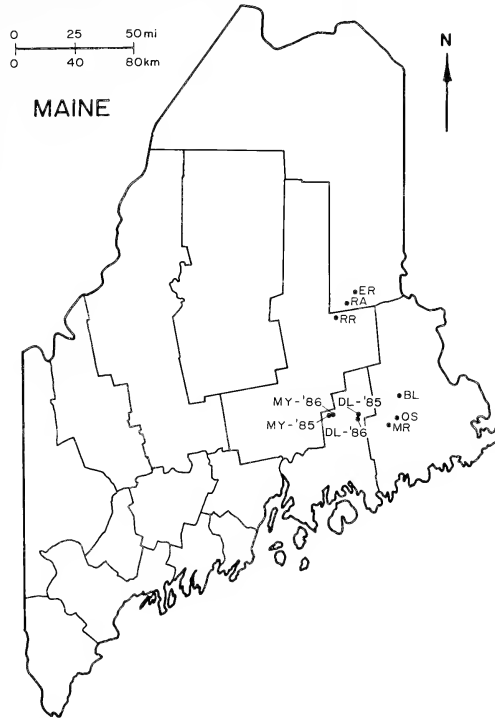


Fig. 1.—Study-site locations in east-central Maine, 1985, 1986. (See text for abbreviations).

ground. Jennings and Collins (1987) found that more spiders were collected when pole pruners were equipped with a catchment basket than with a clamping device (Stein 1969). At ground level, the severed branch and any dislodged arthropods were removed from the basket and placed in a labeled plastic bag for transport to the laboratory.

In the laboratory, trained technicians clipped branches into small lengths (8 to 10 cm) and closely searched all foliage for spruce budworms and spiders. All collected spiders were stored in 2-dram vials containing 75% ethanol.

Spider identifications.—Only sexually mature spiders were identified to species, following identification keys and species descriptions of Kaston (1981) and other consulted sources. Juveniles, including penultimate stages, were identified to generic level, and juveniles of two recognizable species groups (*Philodromus aureolus* and *P. rufus*) were assigned to either group based on color patterns of legs, carapace, and abdomen (Dondale and Redner 1978). Representative specimens of all identified species are deposited in the arachnid collection, U.S. National Museum of Natural History, Washington, DC.

Data analyses.—Branch surface areas were calculated by the formula: $A = (L \times W)/2$, where L is branch length and W is maximum width (Sanders 1980). Population densities were expressed as spiders or spruce budworms/m² of branch foliage area. To estimate absolute populations, we converted spider-budworm densities/m² of foliage area to densities/ha by the method of Morris (1955). Populations were computed as:

$$\text{spiders/ha} = [\bar{X} \text{ spiders/m}^2 \text{ of fir foliage}] \cdot \sum_{F=1}^N \text{BSA}_F +$$

$$\bar{X} \text{ spiders/m}^2 \text{ of spruce foliage} \cdot \sum_{Sp=1}^N \text{BSA}_{Sp}], \text{ where}$$

$$\sum_{F=1}^N \text{BSA}_F = \text{sum of branch surface areas of } N \text{ fir trees/ha;}$$

$$\sum_{Sp=1}^N \text{BSA}_{Sp} = \text{sum of branch surface areas of } N \text{ spruce trees/ha.}$$

The following equations were used to calculate branch surface area per tree based on diameter at breast height (dbh):

$$\text{BSA}_F = -6.93 + 3.43 \text{ dbh}_{\text{cm}}, \text{ after Morris (1955)}$$

$$\text{BSA}_{Sp} = 2.64 + 3.34 \text{ dbh}_{\text{cm}}, \text{ after Dimond (unpubl.)}$$

Nonparametric procedures (Sokal and Rohlf 1981) were used for most statistical tests at $P = 0.05$. The Kruskal-Wallis Test (SAS Institute 1985) was used to compare spider-budworm densities among study sites and between tree species. Pearson correlation coefficient was used to test the interdependence of spider-budworm densities. Regression analyses were used to explore possible relationships between spider populations and measured stand parameters.

RESULTS

Forest stands.—Percentage composition of tree species by basal area (m^2/ha) indicated that most study sites had softwood components of balsam fir and spruces (mostly red spruce) (Table 1), with occasional eastern white pine, eastern hemlock, and northern white-cedar. With few exceptions, hardwoods accounted for $< 30\%$ of total basal area. Deer Lake (DL-85) had a relatively high percentage of eastern hemlock; Myra (MY-86) and Raven (RA) had high percentages of balsam fir.

Mean basal areas of fir and spruces generally were $< 10 \text{ m}^2/\text{ha}$ (Table 2), characteristic of open-grown stands. Mean tree diameters of firs ranged from $9.1 \pm 3.9 \text{ cm}$ to $17.5 \pm 2.2 \text{ cm}$; mean diameters of spruces ranged from $10.7 \pm 0.5 \text{ cm}$ to $29.6 \pm 2.3 \text{ cm}$. Tree heights of dominant/codominant sample trees were 10 to 15 m.

Spider taxa.—Spiders of 11 families, 22 genera, and at least 33 species were collected from arboreal habitats of spruce-fir forests in east-central Maine (Table 3). Fewer families, genera, and species were collected in 1986 than in 1985, but not unexpectedly because only balsam fir was sampled in 1986, and the sampling period was shorter. For both study years, species composition of spiders differed by foraging strategy; species of web spinners were slightly more prevalent in branch samples (56.2% of total species, 1985; 58.8% of total species, 1986) than species of hunters (43.8%, 1985; 41.2%, 1986).

Species per family ranged from one (Linyphiidae, Oxyopidae) to six (Erigonidae). In 1985, equal numbers of species (25) were collected from foliage

Table 1.—Percentage species composition of forest stands investigated for spiders and spruce budworms, east-central Maine, 1985-86.

| Site | Fir | Spruces | Pine | Hemlock | Cedar | Hardwoods |
|------------------|------|---------|------|---------|-------|-----------|
| 1985 Study Sites | | | | | | |
| BL | 27.4 | 15.9 | 15.0 | | 29.2 | 12.4 |
| DL-'85 | 11.1 | 27.8 | 9.3 | 50.0 | | 1.8 |
| ER | 4.3 | 20.5 | | 39.3 | 25.6 | 10.2 |
| MY-'85 | 40.0 | 21.1 | 2.2 | | 1.1 | 35.6 |
| RA | 53.7 | 3.7 | 2.2 | 3.0 | | 37.3 |
| RR | 33.6 | 10.9 | | 29.1 | 0.9 | 25.5 |
| 1986 Study Sites | | | | | | |
| DL-'86 | 44.4 | 41.6 | | | | 13.9 |
| MR | 35.3 | 22.2 | 3.0 | 13.1 | 7.1 | 19.2 |
| MY-'86 | 90.9 | 4.6 | 2.3 | | | 2.3 |
| OS | 45.6 | 14.7 | 7.4 | | 4.4 | 27.9 |

samples of balsam fir and red spruce; only 12 species were collected from foliage of white spruce. In 1986, 17 species were collected from balsam fir foliage, the only tree species sampled that year. Because sampling intensities differed between years, adult spiders of 15 species were collected in 1985 but not in 1986; whereas, adults of only two species, *Mangora placida* (Hentz) and *Eris militaris* (Hentz), were collected in 1986 but not in 1985. Adults of 14 species were collected in both years.

Composition of spider species differed among study sites each year, no doubt because the sites were not identical (Tables 1 and 2) both years. In 1985, adult species per site ranged from 8 to 20 (\bar{X} = 14.3); in 1986, from 6 to 14 (\bar{X} = 10.0). Species common to all six sites sampled in 1985 were *Dictyna brevitaris* Emerton, *Theridion murarium* Emerton, *Pityohyphantes costatus* (Hentz), *Grammonota angusta* Dondale, and *Metaphidippus flaviceps* Kaston. Both *Grammonota pictilis* (O.P.-Cambridge) and *Philodromus exilis* Banks were found on five study sites in 1985. Only one species, *Metaphidippus flaviceps*, was common to all four sites sampled in 1986; however, *Theridion differens* Emerton, *Pityohyphantes costatus*, and *Grammonota angusta* were each found on three sites.

Table 2.—Mean (\pm SE) basal areas of balsam fir and spruces in forest stands investigated for spiders and spruce budworms, east-central Maine, 1985-86. Mean (\pm SE) basal area (m^2/ha).

| Site | Fir | Spruces |
|------------------|------------|-----------|
| 1985 Study Sites | | |
| BL | 7.1 (2.4) | 4.1 (2.2) |
| DL-'85 | 3.4 (2.0) | 8.6 (2.0) |
| ER | 1.2 (0.6) | 5.5 (1.0) |
| MY-'85 | 8.3 (3.1) | 4.4 (1.0) |
| RA | 16.5 (2.3) | 1.2 (0.5) |
| RR | 8.5 (1.7) | 2.8 (1.0) |
| 1986 Study Sites | | |
| DL-'86 | 3.7 (0.5) | 3.4 (0.8) |
| MR | 8.0 (1.0) | 5.0 (1.4) |
| MY-'86 | 9.2 (1.3) | 0.5 (0.3) |
| OS | 7.1 (0.9) | 2.3 (1.0) |

Table 3.—Arboreal spiders on foliage of *Abies balsamea*, *Picea rubens*, and *Picea glauca*, east-central Maine, 1985-86.

| FAMILY <i>Species</i> | BALSAM FIR | | | SPRUCES | | |
|---|------------|-----|------|---------|-----|------|
| | ♂ | ♀ | juv. | ♂ | ♀ | juv. |
| WEB SPINNERS | | | | | | |
| DICTYNIDAE | | | | | | |
| <i>Dictyna brevitorsus</i> Emerton | 6 | 13 | | 5 | 15 | |
| <i>Dictyna phylax</i> Gertsch & Ivie | 2 | 4 | | | 6 | |
| <i>Dictyna</i> sp. | | | 24 | | | 39 |
| THERIDIIDAE | | | | | | |
| <i>Theridion differens</i> Emerton | | 1 | | | | |
| <i>Theridion montanum</i> Emerton | | 3 | | | 4 | |
| <i>Theridion murarium</i> Emerton | 5 | 7 | | 4 | 10 | |
| <i>Theridion</i> sp. | | | 37 | | | 39 |
| LINYPHIIDAE | | | | | | |
| <i>Pityohyphantes costatus</i> (Hentz) | 1 | 10 | | 3 | 8 | |
| <i>Pityohyphantes</i> sp. | | | | | | 7 |
| ERIGONIDAE | | | | | | |
| <i>Ceraticelus atriceps</i> (O.P.-Cambridge) | | 1 | | | | |
| <i>Ceraticelus</i> sp. | | | | | | 1 |
| <i>Dismodicus bifrons decemoculatus</i> (Emerton) | | | | | 1 | |
| <i>Grammonota angusta</i> Dondale | 10 | 56 | | 17 | 59 | |
| <i>Grammonota pictilis</i> (O.P.-Cambridge) | 4 | 10 | | 4 | 11 | |
| <i>Grammonota</i> sp. | | | | | | 5 |
| <i>Pocadicnemis americana</i> Millidge | | | | 1 | 1 | |
| <i>Walckenaeria lepida</i> (Kulczynski) | | 1 | | | | |
| ARANEIDAE | | | | | | |
| <i>Araniella displicata</i> (Hentz) | 3 | 9 | | | 5 | |
| <i>Araniella</i> sp. | | | 1 | | | 3 |
| <i>Araneus</i> sp. (nr. <i>saevus</i>) | | | 1 | | | 1 |
| <i>Araneus</i> sp. | | | 1 | | | |
| <i>Cyclosa conica</i> (Pallas) | | | | | 1 | |
| <i>Cyclosa</i> sp. | | | | | | 1 |
| <i>Mangora placida</i> (Hentz) | | 3 | | | | |
| <i>Neoscona arabesca</i> (Walckenaer) | | | | 1 | | |
| <i>Neoscona</i> sp. | | | 4 | | | 2 |
| TETRAGNATHIDAE | | | | | | |
| <i>Tetragnatha versicolor</i> Walckenaer | | 1 | | 2 | | |
| <i>Tetragnatha viridis</i> Walckenaer | 1 | | | | | 1 |
| <i>Tetragnatha</i> sp. | | | 2 | | | 4 |
| Subtotals | 32 | 119 | 70 | 37 | 121 | 103 |
| HUNTERS | | | | | | |
| OXYOPIDAE | | | | | | |
| <i>Oxyopes</i> sp. | | | 1 | | | |
| CLUBIONIDAE | | | | | | |
| <i>Clubiona canadensis</i> Emerton | | 2 | | | 1 | |
| <i>Clubiona trivialis</i> C. L. Koch | 1 | 1 | | | | |
| <i>Clubiona</i> sp. | | | 4 | | | 11 |
| PHILODROMIDAE | | | | | | |
| <i>Philodromus exilis</i> Banks | 1 | 6 | | 2 | 6 | |
| <i>Philodromus pernix</i> Blackwall | | 1 | | | 3 | |
| <i>Philodromus placidus</i> Banks | | 5 | | | 6 | |
| <i>Philodromus praelustris</i> Keyserling | | | | 1 | | |
| <i>Philodromus rufus vibrans</i> Dondale | | 1 | | | | |
| <i>Philodromus</i> sp. (<i>aureolus</i> grp.) | | | 3 | | | 1 |

| | | | | | | |
|---|----|-----|-----|----|-----|-----|
| <i>Philodromus</i> sp. (<i>rufus</i> grp.) | | | 14 | | | 26 |
| <i>Philodromus</i> sp. | | | 15 | | | 33 |
| THOMISIDAE | | | | | | |
| <i>Misumena vatia</i> (Clerck) | 1 | 1 | | | | |
| <i>Misumena</i> sp. | | | | | | 1 |
| <i>Xysticus punctatus</i> Keyserling | | 4 | | 2 | 1 | |
| <i>Xysticus</i> sp. | | | 19 | | | 40 |
| SALTICIDAE | | | | | | |
| <i>Eris militaris</i> (Hentz) | 1 | 1 | | | | |
| <i>Eris</i> sp. | | | 1 | | | |
| <i>Metaphidippus flaviceps</i> Kaston | 6 | 23 | | 6 | 13 | |
| <i>Metaphidippus protervus</i> (Walckenaer) | | | | 1 | | |
| <i>Metaphidippus</i> sp. | | | 47 | | | 64 |
| <i>Salticus scenicus</i> (L.) | | 1 | | | | |
| Subtotals | 10 | 46 | 104 | 12 | 30 | 176 |
| TOTALS | 42 | 165 | 174 | 49 | 151 | 279 |

Spider numbers, life stages, sex ratios.—Over half (62.6%) of the total collected spiders ($n = 765$) in 1985 were from spruces. This high percentage was unexpected because of the distribution of branch samples among tree species in 1985, i.e., balsam fir ($n = 60$), red spruce ($n = 50$), and white spruce ($n = 10$). In 1986, all of the collected spiders ($n = 95$) were from balsam fir trees ($n = 80$).

In 1985, most collected spiders were juveniles (53.6%), followed by females (35.7%), and males (10.7%). In 1986, both juveniles and females were equally abundant (45.3% each) among collections, with fewer males (9.5%). Sex ratios of males to females were 1:3.3 in 1985 and 1:4.8 in 1986.

Spider densities.—For both study years, spider populations/ m^2 of foliage area varied among study sites (Tables 4 and 5, column \bar{X} 's). In 1985, most sites had comparable means of 10 to 14 spiders/ m^2 of balsam fir foliage and 19 to 20 spiders/ m^2 of spruce foliage. In 1986, most sites had means of 7 to 14 spiders/ m^2 of balsam fir foliage; spruce was not sampled that year. For unknown reasons, some sites had significantly fewer spiders (balsam fir-RA, DL-86; spruces-ER, RA) than other sites.

Spider densities/ m^2 of foliage generally were greater on spruces than on balsam fir (Table 4, row \bar{X} 's); these differences were significantly greater ($P \geq 0.05$) on three of the study sites and over all sites in 1985. However, guild densities by foraging strategy (web spinner, hunter) were not significantly different ($P \geq 0.05$) among tree species in 1985.

Budworm densities.—Populations of spruce budworm larvae and pupae/ m^2 of foliage also varied among study sites both years (Tables 4 and 5, column \bar{X} 's). In 1985, mean densities were about equal between host tree species for most sites and over all sites. In 1986, most study sites had mean densities > 200 budworms/ m^2 of balsam fir foliage; all sites $\bar{X} = 224.4 (\pm 10.4)$.

Absolute populations.—Estimates of arboreal spiders/ha ranged from 80,745 ($\pm 17,643$) to 323,080 ($\pm 114,839$) in 1985 [$\bar{X} = 192,073 (\pm 28,171)$]; from 35,139 ($\pm 5,338$) to 287,024 ($\pm 40,853$) [$\bar{X} = 175,047 (\pm 20,287)$] in 1986. Some of the observed variation among sites may be attributed to differences in percentage species composition of balsam fir and spruces (Table 1); however, spider densities/ha were weakly correlated with percentage fir ($r = -0.08$, 1985; $r = 0.03$, 1986), but more closely with percentage spruce ($r = 0.30$, 1985). Differences in percentages of balsam fir and spruces profoundly affected estimates of spiders/ha

Table 4.—Densities of spiders and spruce budworms/m² of foliage, balsam fir, red and white spruces, east-central Maine, 1985. *=White spruce sampled on MY-'85; red spruce sampled on all other sites. Column means (ab) followed by the same letter(s) are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$. Row means (xy) followed by the same letter(s) are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$.

| 1985 SITES | SPIDERS $\bar{X}(\pm SE)/m^2$ | | SPRUCE BUDWORMS $\bar{X}(\pm SE)/m^2$ | |
|------------|-------------------------------|--------------|---------------------------------------|-----------------|
| | Balsam fir | Spruces* | Balsam fir | Spruces* |
| BL | 13.9ax (2.5) | 20.2ay (2.7) | 146.1bx (17.2) | 99.4cy (11.5) |
| DL-'85 | 10.6ax (1.8) | 20.4ay (3.2) | 167.7bx (22.6) | 179.4bx (28.0) |
| ER | 10.5ax (3.8) | 9.6bx (1.9) | 54.8cx (11.9) | 25.8dx (4.2) |
| MY-'85 | 12.7ax (2.4) | 19.0ay (2.6) | 212.6ax (21.9) | 217.6ax (21.5) |
| RA | 3.3bx (0.8) | 8.4bx (1.8) | 35.2cx (4.5) | 34.3dx (6.3) |
| RR | 14.3ax (2.4) | 18.9ax (2.9) | 145.6bx (17.5) | 130.7bcx (14.6) |
| ALL | 10.9x (1.0) | 16.3y (1.1) | 129.9x (7.8) | 117.8x (7.9) |

between tree species on the same site. For example, although spiders/m² of foliage were not significantly different between sampled tree species for study site ER in 1985 (Table 4), significantly more ($P \leq 0.03$) spiders/ha were estimated to occur on spruces than on balsam fir, largely due to the preponderance of spruces ($5X > \text{fir}$) on this site. The same pattern of influence also was evident for balsam fir; however, when host-tree differences were $\leq 2X$, then spider densities/ha tended to equalize between tree species.

Estimates of absolute populations of spruce budworms/ha ranged from 271,401 ($\pm 67,590$) to 3,076,290 ($\pm 928,941$) in 1985 [$\bar{X} = 1,821,159$ ($\pm 273,181$)]; from 2,465,473 ($\pm 347,069$) to 6,122,919 ($\pm 1,091,369$) in 1986 [$\bar{X} = 4,258,870$ ($\pm 422,723$)].

Spider-budworm relationships.—Correlation analyses indicated positive significant associations between spider and budworm densities/ha each study year (Figs. 2 and 3). Spider and budworm densities covaried slightly more together in 1985 ($r = 0.84$, $P \leq 0.001$) than in 1986 ($r = 0.71$, $P \leq 0.001$), which might be attributed to population estimates derived from only one tree species in 1986. The scattered data points at relatively high spider-budworm densities (i.e., $\geq 400,000$ spiders, ≥ 4.5 million budworms) indicated greater variation above these densities in 1985 (Fig. 2) than in 1986 (Fig. 3).

Spider/forest stands.—Regression analyses indicated that none of the measured forest-stand parameters were reliable predictors of spider populations/ha (Table 6). For unknown reasons, total basal area, fir basal area, and percent spruce were better indicators (i.e., higher r^2 values) of spider populations in 1986 than in 1985.

Table 5.—Densities of spiders and spruce budworms/m² foliage, balsam fir, east-central Maine, 1986. Column means (ab) followed by the same letter are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$.

| 1986 SITES | SPIDERS $\bar{X}(\pm SE)/m^2$ | SPRUCE BUDWORMS $\bar{X}(\pm SE)/m^2$ |
|------------|-------------------------------|---------------------------------------|
| DL-86 | 3.2b (1.0) | 289.9a (20.7) |
| MR | 9.4a (2.2) | 118.6b (11.5) |
| MY-'86 | 7.0a (1.6) | 235.2a (17.5) |
| OS | 13.9a (2.4) | 255.8a (24.6) |
| ALL | 8.5 (1.0) | 224.4 (10.4) |

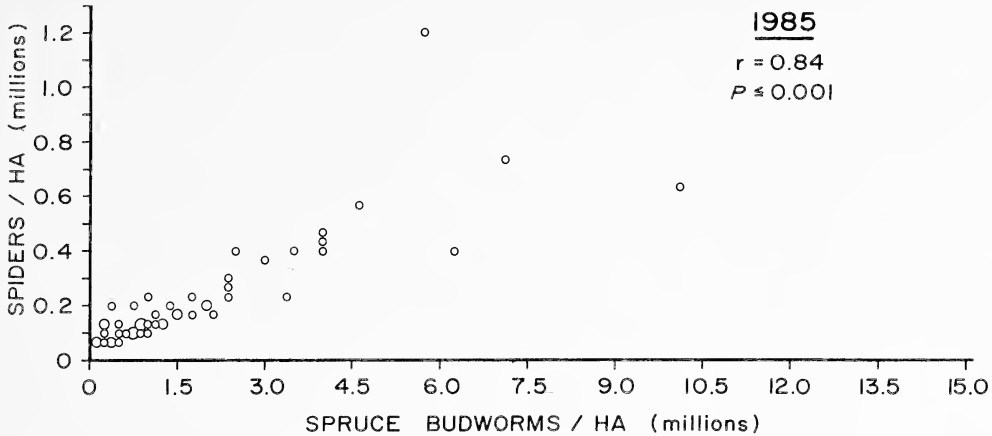


Fig. 2.—Association of spider-budworm densities per hectare, six study sites, east-central Maine, 1985. (Pearson Correlation Coefficient, $r = 0.84$, $P \leq 0.001$). Small, medium, and large circles represent one, two, and three observations, respectively.

DISCUSSION

Spider taxa.—Many of the species of spiders we collected on foliage of balsam fir, red and white spruces in east-central Maine have been taken on balsam fir in New Brunswick (Loughton et al. 1963; Renault 1968) and on red spruce in northern Maine (Jennings and Collins 1987). Species not previously recorded from arboreal habitats of Maine's spruce-fir forests include *Pocadicnemis americana* Millidge, *Walckenaeria lepida* (Kulczynski), *Tetragnatha viridis* Walckenaer, *Philodromus praelustris* Keyserling, *Eris militaris* (Hentz), and *Metaphidippus flaviceps* Kaston.

Based on frequency of collection (this study and Loughton et al. 1963; Renault 1968; Renault and Miller 1972; Jennings and Collins 1987), we consider the following species as typical arboreal spiders of northeastern spruce-fir forests: *Dictyna brevitaris* Emerton, *D. phylax* Gertsch & Ivie, *Theridion montanum* Emerton, *T. murarium* Emerton, *Pityohyphantes costatus* (Hentz), *Ceraticelus atriceps* (O.P.-Cambridge), *Grammonota angusta* Dondale, *Araniella displicata* (Hentz), *Clubiona canadensis* Emerton, *C. trivialis* C. L. Koch, *Philodromus exilis* Banks, *P. placidus* Banks, and *Xysticus punctatus* Keyserling.

Our observed differences in composition of spider species by foraging strategy (web spinners, 55%; hunters, 45%) generally agree with earlier studies. Jennings and Collins (1987) collected more species of web spinners (54%) than hunters (46%) from red spruce foliage in northern Maine ($n = 21$ species). Likewise, Jennings and Hilburn (1988) captured more species of web spinners (56%) than hunters (44%) in Malaise traps operated in spruce-fir forests of west-central Maine ($n = 25$ species). Even greater percentages of web spinners (67%) than hunters (33%) were reported associated with balsam fir foliage in New Brunswick, where $n = 54$ species (Loughton et al. 1963). We conclude that the web-spinner guild comprises a major species component of the arboreal spider fauna associated with northeastern spruce-fir forests.

The observed dissimilarities in composition of spider species among study sites may be within the realm of expected variation for northeastern spruce-fir forests.

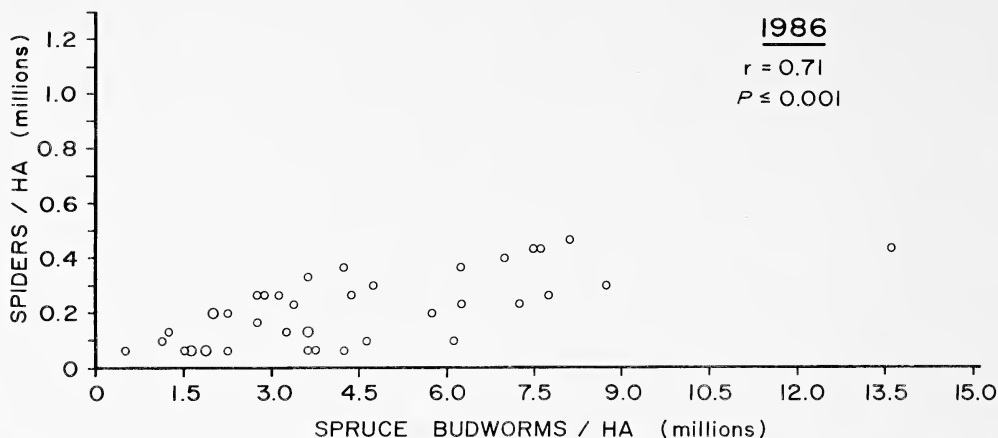


Fig. 3.—Association of spider-budworm densities/ha, four study sites, east-central Maine, 1986. (Pearson Correlation Coefficient, $r = 0.71$, $P \leq 0.001$). Small, medium, and large circles represent one, two, and three observations, respectively.

Renault and Miller (1972:1045-46) noted "a remarkable constancy in the species composition in any one location," but "a marked dissimilarity in the species composition in different areas," all classed as fir-spruce biotype. Until additional studies are completed, the overall species composition of arboreal spruce-fir spiders remains undefined except for localized areas. No doubt, additional species will be added to the known fauna by the use of other sampling methods (e.g., whole-tree counts), extension of sampling periods, and increased sample sizes.

Spider numbers, life stages, sex ratios.—Some of the observed differences in spider numbers, life stages, and sex ratios can be attributed to reproductive cycles of individual species and production of young spiderlings during midsummer. At least five of the species found during this study, *Theridion murarium* Emerton, *Araniella displicata* (Hentz), *Misumena vatia* (Clerck), *Xysticus punctatus* Keyserling, and *Philodromus placidus*, have biennial life histories (Dondale 1961, 1977). Juveniles of *Theridion*, *Xysticus*, and *Philodromus* commonly were collected among branch samples, especially in 1985, and probably represented immature stages of biennial species.

The biased sex ratio in favor of females was not unexpected because female spiders generally live longer than males (Gertsch 1979), and males generally are more vagrant and hence less likely to be sampled than females. However, we are unable to explain why female spiders were slightly more prevalent among collections in 1986 (45.3%) than in 1985 (35.7%). Sample size (i.e., 878 branches in 1985 vs. only 298 branches in 1986) and sampling-time differences between years may have been contributing factors.

Spider densities.—The spider densities/ m^2 of foliage that we observed in east-central Maine generally are greater than those previously reported elsewhere. Morris (1963) noted densities of 2.65 spiders/ 10 ft^2 ($2.85/m^2$) of balsam fir foliage in June and 2.34 spiders/ 10 ft^2 ($2.52/m^2$) in July, on the Green River Watershed, New Brunswick. For two plots on the same watershed and sampling dates comparable to our Maine study (22 May to 12 July), Loughton et al. (1963) reported densities ranging from 0.6 spiders/ 10 ft^2 ($0.6/m^2$) to 18.9 spiders/ 10 ft^2 ($20.3/m^2$) of balsam fir foliage. We calculated mean densities for these same plots and sampling periods as: K2 = 9.5 spiders/ m^2 (1957), 7.9 spiders/ m^2 (1958); G16 =

Table 6.—Coefficients of determination (r^2) for predicting spider populations/ha based on forest stand parameters.

| STAND PARAMETER | 1985 | | 1986 | |
|-------------------|-------|------|-------|------|
| | r^2 | P | r^2 | P |
| Total basal area | 0.06 | 0.65 | 0.31 | 0.44 |
| Fir basal area | 0.03 | 0.73 | 0.48 | 0.31 |
| Spruce basal area | 0.08 | 0.59 | 0.04 | 0.81 |
| Percent fir | 0.01 | 0.88 | 0.00 | 0.97 |
| Percent spruce | 0.09 | 0.56 | 0.56 | 0.25 |

7.9 spiders/m² (1957), 5.6 spiders/m² (1958). Renault and Miller (1972) noted a yearly constancy of about 8.2 spiders/m² of balsam fir foliage for a 9-year period (1962-70), on the Green River Watershed, New Brunswick.

For spiders on spruces, Morris (1963) reported densities of 4.8 spiders/10 ft² (5.2/m²) in June and 12.5 spiders/10 ft² (13.4/m²) in July, Green River Watershed, New Brunswick. In northern Maine, Jennings and Collins (1987) observed densities ranging from 1.5 to 16.6 spiders/m² and a mean density of 7.1 spiders/m² of red spruce foliage sampled in late July. The overall mean density of 16.3 spiders/m² of spruce foliage in east-central Maine was substantially greater than expected based on previous studies.

Absolute populations.—Our estimates of absolute populations of arboreal spiders/ha generally were less than some earlier findings, i.e., Morris (1963) estimated 187,500 spiders/ha in New Brunswick; Haynes and Sisojevic (1966) estimated 312,500/ha in New Brunswick; Jennings and Collins (1987) estimated 645,853/ha in north-central Maine. We suspect that stand species composition and stand density are important determinants of absolute populations of arboreal spiders. For example, the sites investigated in east-central Maine were open grown, fir-spruce stands; whereas, those estimated to harbor 645,853 spiders/ha were dense, red spruce stands (Jennings and Collins 1987). No doubt our estimates and those earlier are conservative because not all represented tree species were sampled. Total absolute populations of spiders/ha are apt to be much higher when estimates include all tree species and all strata (arboreal, epigeal, terrestrial).

Spider-budworm relationships.—Based on the observed high correlations between spider and budworm densities, we suspect that spiders were responding to available prey (budworm) populations in east-central Maine. All life stages of the spruce budworm—eggs, larvae, pupae, and adults—are susceptible to spider predation, but the larvae are particularly vulnerable because of their relative abundance, size, and activity. Loughton et al. (1963) investigated spider predation on the spruce budworm in New Brunswick and concluded that: (1) erigonids are the most important predatory group because of their large numbers; (2) theridiids are the most effective predators, based on percentages showing positive feedings on budworm; and (3) salticids are important predators at all stages of budworm larval development, including the late instars. Predation on the large larvae is especially important because mortality during the late larval stage influences generation survival of the spruce budworm (Morris 1963). All three spider families (Erigonidae, Theridiidae, Salticidae) were common among branch samples from balsam fir and spruces in east-central Maine.

Spiders/forest stands.—Small sample sizes ($n = 6$ sites, 1985; $n = 4$ sites, 1986) may have contributed to the weak relationships between forest-stand parameters and estimates of spider populations/ha in east-central Maine. Because of greater spider densities and lower coefficients of variation on spruce, we predict that percentage spruce will be a more reliable indicator of absolute spider populations/ha than percentage fir. However, numerous other factors, such as canopy closure, crown class, and stand age, warrant investigation.

Jennings and Collins (1987) hypothesized that red spruce may harbor more spiders, both individuals and species, than balsam fir. Our results in east-central Maine partially support this hypothesis, i.e., overall, significantly more ($P \leq 0.001$) spiders/m² of foliage were found on spruces (red, white) than on balsam fir. We also found equal numbers of spider species (25) despite unequal sample sizes in favor of balsam fir. We suspect that additional spider species may occur on each tree species and that spruces provide greater microhabitat space for web building and for foraging by hunting spiders. In Minnesota, Stratton et al. (1979) found that white spruce had more spider individuals and species than red pine, *Pinus resinosa* Ait., and northern white-cedar. They attributed the greater spider diversity on spruce to differences in plant physiognomy, i.e., structure of needles and branches.

Results of our study in east-central Maine indicate that: (1) host-tree species influences arboreal-spider density per m² of foliage area, (2) percentage composition of tree species in forest stands affects overall estimates of arboreal-spider populations/ha, and (3) estimates of spider-budworm (predator-prey) densities may be highly correlated. Additional studies are needed to define and evaluate other factors that possibly influence spider populations on northeastern conifers. If indeed spruce supports greater populations of spiders than fir, forest pest managers will have the option to manage forests to increase populations of potential predators of the spruce budworm. Such options offer alternatives to reliance solely on chemical insecticides.

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MORPHOLOGY OF THE DORSAL INTEGUMENT OF TEN OPILIONID SPECIES (ARACHNIDA, OPILIONES)

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ABSTRACT

Specimens of *Siro exilis* Hoffman, *Vonones sayi* (Simon), *Erebomaster* sp., *Leiobunum vittatum* (Say), *Leiobunum holtae* McGhee, *Hadrobunus maculosus* (Wood), *Eumesosoma nigrum* (Say), *Odiellus pictus* (Wood), *Caddo agilis* Banks, and *Hesperonemastoma kepharti* (Crosby and Bishop) were investigated using scanning electron microscopy. Features of the dorsal integument of each specimen are described using available terminology. Variations in the generalized tuberculate-granulate morphology were observed in eight of the ten species studied. *V. sayi*, *C. agilis*, and *O. pictus* exhibit a morphological gradient in features of their dorsal integuments. The presence of micropores is reported from the apices of tubercles of *L. vittatum*, *L. holtae*, *H. maculosus*, and *O. pictus* and from the cuticular backgrounds of *S. exilis*, *V. sayi*, and *E. nigrum*. The morphological descriptions and comparisons presented provide a terminology for describing opilionid cuticular features.

INTRODUCTION

Species of the order Opiliones are often characterized by prominent protuberances, spines, and ornamented cuticles, especially in the suborder Laniatores (Shear and Gruber 1983). Studies with scanning electron microscopy (SEM) reveal still other, smaller, cuticular features. In the past, morphological studies of arthropod integuments have been primarily limited to insects. Although various morphological descriptions of the arachnid cuticle exist in the literature, a consistent descriptive terminology is currently unavailable.

Previous light microscopical studies of arachnid integuments include those of Edgar (1963), Immel (1964), Grainge and Pearson (1966), Kennaugh (1968), Dalingwater (1975, 1981, 1987), and van der Hammen (1985), among others. Selected SEM studies of arachnid taxa exclusive of the Opiliones include those of Brody (1970), Pittard and Mitchell (1972), Woolley (1974), Crowe (1975), Quintero (1975), Platnick and Gertsch (1976), Platnick and Shadab (1976), Mutvei (1977), Keirans and Clifford (1978), Hill (1979), Hadley and Filshie (1979), Emerit (1981), Hadley (1981), Opell (1983), Platnick (1986), and Igelmund (1987). SEM studies of various opilionid species were conducted by Juberthie and Massoud (1976), Martens (1979), Martens and Schawaller (1977), and Spicer (1987). Martens (1978) referred to both macro- and micromorphological features

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of the opilionid integument. Shear (1986) and Shear and Gruber (1983) used SEM to illustrate characters for cladistic analysis of ischyropsalidoid and troguloid opilionids.

The purpose of this paper is to illustrate the cuticular features of ten opilionid species, propose a descriptive terminology for these features, and make preliminary comparisons of related species based on their cuticular features.

METHODS AND MATERIALS

Sources of material.—Specimens were obtained from the private collection of Dr. Charles R. McGhee at Middle Tennessee State University and from localities in Rutherford, Bedford, Cannon, McMinn, and Hickman counties of Tennessee. One species, *Eumesosoma nigrum* (Say), was on loan from the American Museum of Natural History.

Method of study.—All specimens were preserved in 70% ethanol prior to preparation for SEM. The specimens were allowed to air dry or were freeze-dried from quick-frozen distilled water using a Thermovac lyophilizer. Freeze-drying was used for those species whose cuticles became distorted with air desiccation.

The dried specimens were mounted on aluminum stubs using an epoxy glue for larger specimens and double-stick adhesive tape for smaller specimens, coated with gold-palladium in a Technics Hummer VI sputtering system, and examined at an accelerating voltage of 15 kV in an ISI SX-30 SEM. Photomicrographs were made with a Pentax MX 35 mm camera using Kodak™ Plus-X film.

The surface features illustrated by the photomicrographs were compared with existing micrographs and morphological descriptions of both arachnid and insect integuments in an attempt to apply an appropriate descriptive terminology. The investigations of Harris (1979), Byers and Hinks (1973), Hinton (1970), and Kennaugh (1968) as well as the general works of Torre-Bueno (1962), Steinmann and Zombori (1981), and Baker and Wharton (1952) were used as primary sources of descriptive terminology.

Magnification and terminology.—The photomicrographs are reproduced at magnifications which best illustrate the proposed terminology. Measurements in micrometers (um) are given to provide size comparisons.

Because many descriptive terms exist with both diminutive and superlative forms, micromorphological descriptions require standards for selecting proper terms. The author agrees with Shear and Gruber (1983) who used the prefix "micro-" preceding terms describing features which measure 0.01 mm or less in size. Often, a species' integument is sufficiently detailed to warrant the use of two, rarely three, descriptive components. This procedure is favored over the arbitrary creation of terms in a field often burdened with excessive synonymy.

RESULTS

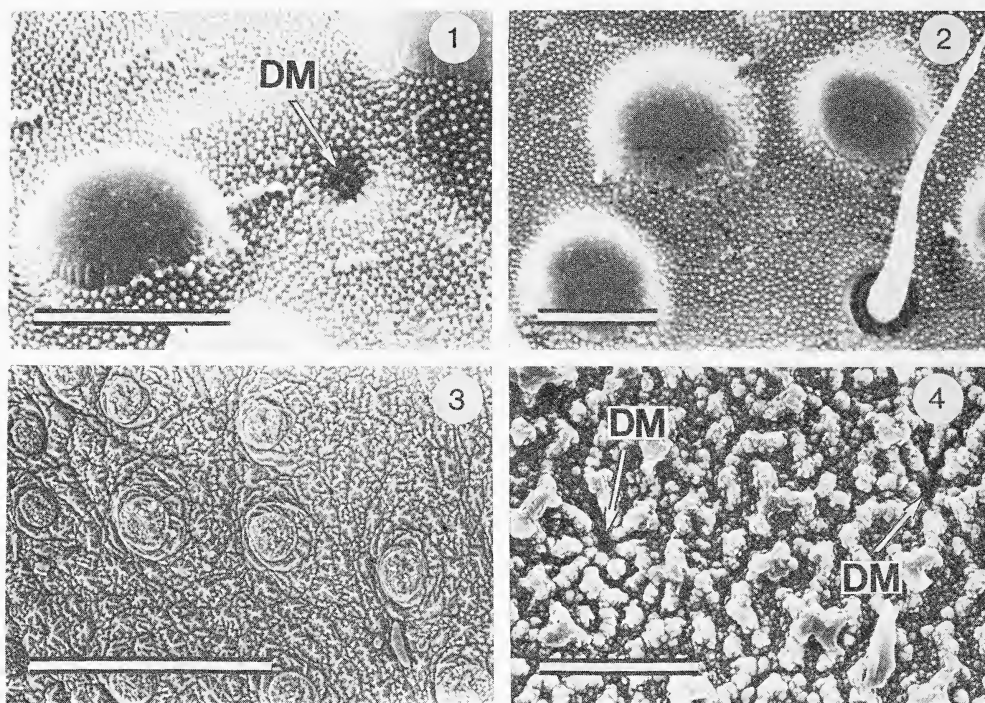
The features of the dorsal integument of ten opilionid species representing nine genera and six families within the three suborders of the Opiliones were examined and described (Table 1). No cuticular differences attributable to sexual dimorphism were observed in species for which both sexes were available for study. A systematic list of the species studied is given in Appendix 1. Cuticular

Table 1.—A summary of the cuticular features of 10 opilionid species. Refer to Appendix 1 for higher taxonomy.

| | <i>S. exilis</i> | <i>V. sayi</i> | <i>E. sp.</i> | <i>L. vitt.</i> | <i>L. holt.</i> | <i>H. mac.</i> | <i>E. nig.</i> | <i>O. pic.</i> | <i>C. agilis</i> | <i>H. kepharti</i> |
|------------------------|------------------|----------------|---------------|-----------------|-----------------|----------------|----------------|----------------|------------------|--------------------|
| Tuberculate | X | X | | X | X | X | X | X | | |
| Convex | X | | | | | | | | | |
| Rounded | | | | X | X | X | | X | | |
| Basally constricted | | | | | | | X | | | |
| Microgranulate | | X | | | | | | | | |
| Laminate | | | | X | X | X | | X | | |
| Spirally | | | | X | X | X | | | | |
| Perpendicularly | | | | | | | | X | | |
| Glabrous | | | | | | | | X | | |
| Microtuberculate | | | X | | | | | | X | X |
| Convex | | | X | | | | | | | |
| Oblong | | | | | | | | | | X |
| Obtuse/subdeltoid | | | | | | | | | X | |
| Reticulate | | | X | | | | | | | |
| Microgranulate | | | | | | | | | | X |
| Denticles | | | | | | X | | | | |
| Micropores | X | X | | | | | X | X | | |
| On tubercles | | | | X | X | X | | X | | |
| Not on tubercles | X | X | | | | | X | | | |
| Foveolate | X | X | | | | | X | | | |
| Cycloid facetodea | | X | X | | | X | | X | X | |
| Microgranulate | X | X | X | X | X | X | X | | | X |
| Two-ranked | X | | | | | | | | | |
| Dentate | | | | X | X | X | X | | | |
| Imbricate | | X | | | | | | X | X | |
| Subimbricate | | X | | | | | | | X | |
| Laminate | | X | | | | | | X | | |
| Acute/obtuse | | X | | | | | | X | | |
| Keeled | | X | | | | | | X | | |
| Mucronate | | | | | | | | X | | |
| Reticulate | | | | | | | | X | | |
| Rivulose | | X | X | | | | | | | |
| Rugose-plicate | | | | | | | | | X | |
| Sinuate | | X | | | | | | | | |
| Striate | | | | | | | | | X | |
| Rectilinear setae | X | | X | | | | | | | |
| Arcuate setae | | X | | X | X | X | X | X | X | X |
| Substrate setae | | X | | X | X | X | X | | X | X |
| Spirally | | X | | X | X | X | X | | X | X |
| Setae on areolae | | X | X | | | | | | | |
| Torose areolae | | X | | | | | | | | |
| Setae on microareolae | | | | X | X | X | X | | X | X |
| Rounded | | | | X | X | X | | | | X |
| Depressed | | | | | | | X | | X | |
| Setae on microalveolae | X | | | | | | | | | |

comparisons between related species (see Discussion) are made to better distinguish the characters of each species and are not intended to show phylogenetic relationships. Applied descriptive terminology is defined in Appendix 2.

***Siro exilis* Hoffman.**—*Dorsal integument:* A tuberculate-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 1). The convex tubercles are smooth above with abbreviated



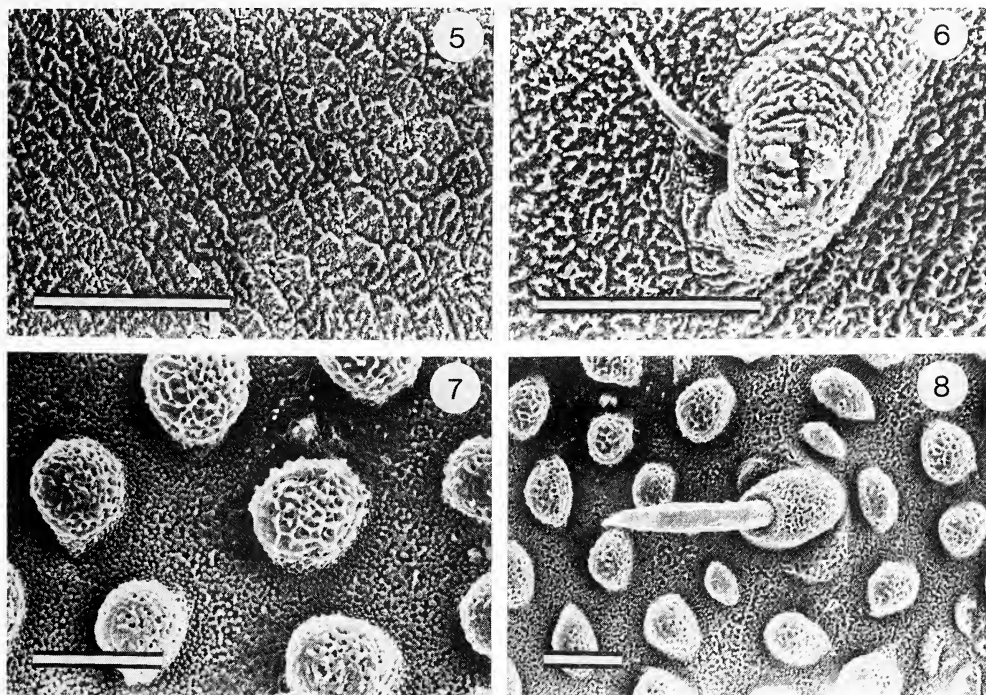
Figs. 1-4—Opilionid dorsal integument morphology: 1-2, *S. exilis*; 1, dermal gland micropore (DM); 2, abdominal seta; 3-4, *V. sayi*, 3, anterior cephalothorax; 4, posterior cephalothorax with dermal micropores. Scale = 10 μm , except Fig. 3, 100 μm .

microstriae surrounding their bases. The microgranulations of the cuticular background are regularly spaced, two-ranked, and appear as rounded points. The larger microgranulations measure 0.5 μm in basal diameter and as many as 40 are present in a given 25 μm^2 . The smaller microgranulations measure 0.25 μm in basal diameter and as many as 70 are represented in 25 μm^2 . The openings of dermal gland micropores (Juberthie and Massoud 1976) are seen as microfoveolae (Fig. 1). Each opening is encircled by 15-17 of the larger microgranulations.

Abdominal setae: Rectilinear-acicular setae arise from depressed microalveolae (Fig. 2).

Vonones sayi (Simon).—*Dorsal integument*: The anterior cephalothoracic region exhibits a tuberculate-rivulose-microgranulate morphology (Fig. 3). The tubercles are located anterior to the ocularium and appear as rounded microgranular elevations of the cuticle. No micropores are visible on the surfaces of the tubercles. The cuticular surface has a subimbricate background of polygonal plates which exhibit a pattern of microgranular, sinuate furrows. The furrows are in relief of non-parallel ridges formed by fusion of the microgranulations. Numerous micropores appear as foveolae and are encircled by microgranulations. The microgranulations vary considerably in size and shape, with a maximum basal diameter of 0.4 μm .

Both the posterior cephalothoracic and anterior abdominal regions exhibit a rivulose-microgranulate morphology (Fig. 4) which closely resembles that of the anterior cephalothorax, with the exception that no tubercles or polygonal plates are seen. The openings of micropores are also seen in this region.



Figs. 5-8—Opilionid dorsal integument morphology: 5-6, *V. sayi*; 5, posterior abdomen; 6, cephalothoracic seta; 7-8, *Erebmaster* sp.; 7, dorsum; 8, abdominal seta. Scale = 50 μ m (Figs. 5-6), 10 μ m (Figs. 7-8).

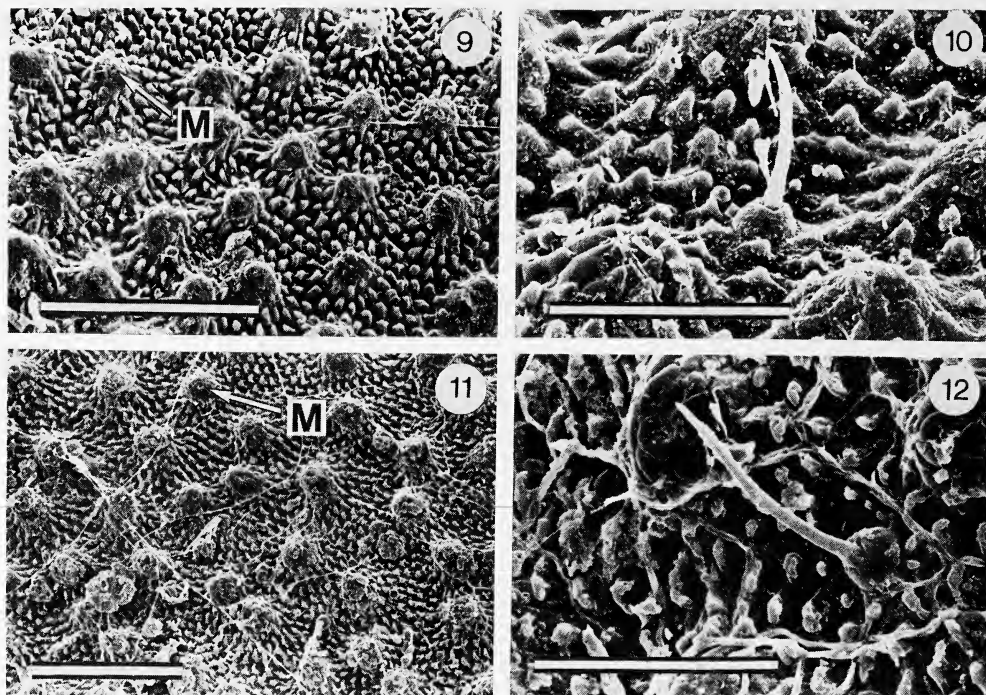
The posterior abdominal region of *V. sayi* is imbricate-rivulose-microgranulate (Fig. 5). The imbrications or laminae are essentially similar to the polygonal plates of the anterior cephalothoracic region. The laminae are, however, keeled distally and range from obtuse to acute. Micropores also are seen in this region.

Cephalothoracic setae: Arcuate-acicular setae lie parallel to the surface of the integument (Fig. 6). The setae are spirally substriate with basal, torose areolae which are rivulose-microgranulate. Setae are found only in the lateral areas of the cephalothorax, in certain areas of the posterior abdomen, and on the appendages.

***Erebmaster* sp.—Dorsal integument:** A microtuberculate-rivulose-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 7). The numerous, convex microtubercles are superficially reticulate in some cases while others exhibit a punctulate morphology. The microgranulations of the cuticular background are of variable size and shape and have a maximum basal diameter of 0.1 μ m. Abbreviated asymmetrical ridges are formed by fusion of the microgranulations. Micropores, if present, can not be distinguished from either the punctulations of the microtubercles or the coalescent microgranular background.

Abdominal setae: Rectilinear, thick-shafted setae lie parallel to the surface of the integument (Fig. 8). The setae have prominent basal areolae which, like the microtubercles, are rivulose-microgranulate.

***Leiobunum vittatum* (Say).—Dorsal integument:** A tuberculate-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 9). The tubercles appear as rounded elevations of the cuticle and



Figs. 9-12.—Opilionid dorsal integument morphology: 9-10, *L. vittatum*; 9, micropore (M); 10, abdominal setae; 11-12, *L. holtae*; 11, micropore; 12, abdominal seta. Scale = 50 μm (Figs. 10, 12), 100 μm (Figs. 9, 11).

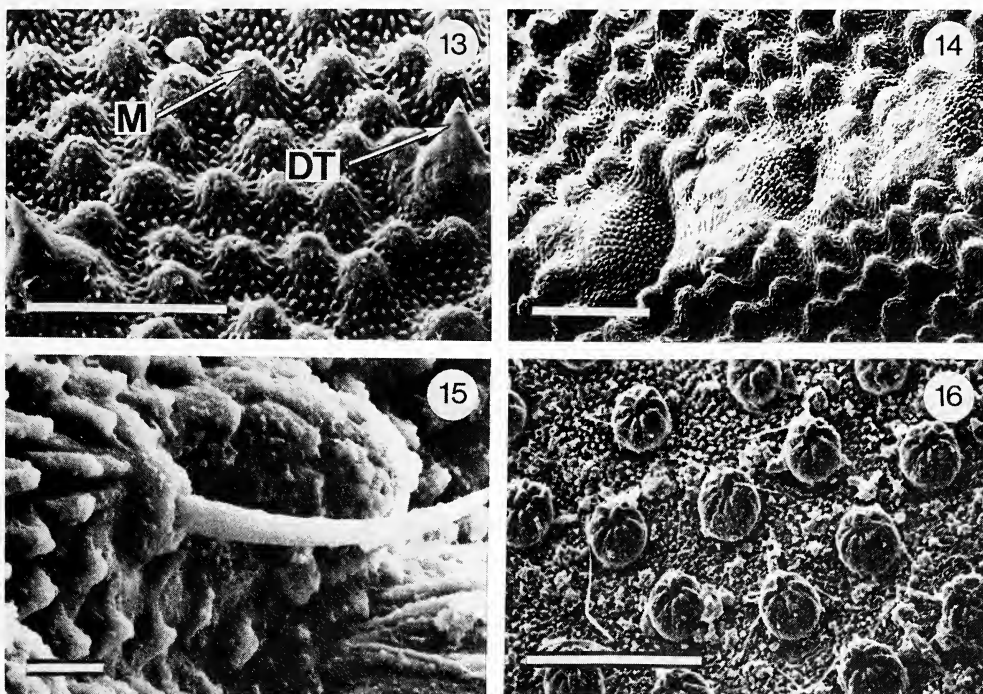
are covered by a number of laminae which form a loosely aggregated spiral. A micropore is visible at the summit of each tubercle. The microgranulations are subequal in size and appear as dentate projections of the integument. The basal width of the microgranulations ranges from 5 to 8 μm . The less sclerotized, transverse and lateral areas of the dorsum are microgranulate and devoid of tubercles.

Abdominal setae: Thick-shafted, arcuate-acicular setae arise from rounded microareolae which do not resemble the larger tubercles or the smaller microgranulations (Fig. 10). The setae are spirally substriate.

***Leiobunum holtae* McGhee.**—**Dorsal integument:** As illustrated in Fig. 11, both the cephalothoracic and abdominal tergites of this species are tuberculate-microgranulate. The cuticular morphology closely resembles that of *L. vittatum*. All regions of the dorsal integument of *L. holtae* exhibit both tubercles and microgranulations.

Abdominal setae: As illustrated in Fig. 12, the setae of *L. holtae* closely resemble those of *L. vittatum*.

***Hadrobunus maculosus* (Wood).**—**Dorsal integument:** A tuberculate-microgranulate morphology is exhibited by both the cephalothoracic and abdominal tergites of this species (Fig. 13). The cuticular morphology closely resembles that of the two *Leiobunum* species with the exception of smooth, pointed denticles which are sparsely distributed. The denticles measure approximately 50 μm in height and 40 μm in basal width. Tubercles, denticles, and microgranulations are observed from all regions of the dorsal integument. Numerous circular structures consisting of



Figs. 13-16.—Opilionid dorsal integument morphology: 13-15, *H. maculosus*; 13, micropore (M) and denticle (DT); 14, cycloid facetodea; 15, abdominal seta; 16, *E. nigrum*. Scale = 100 μm , except Fig. 15, 10 μm .

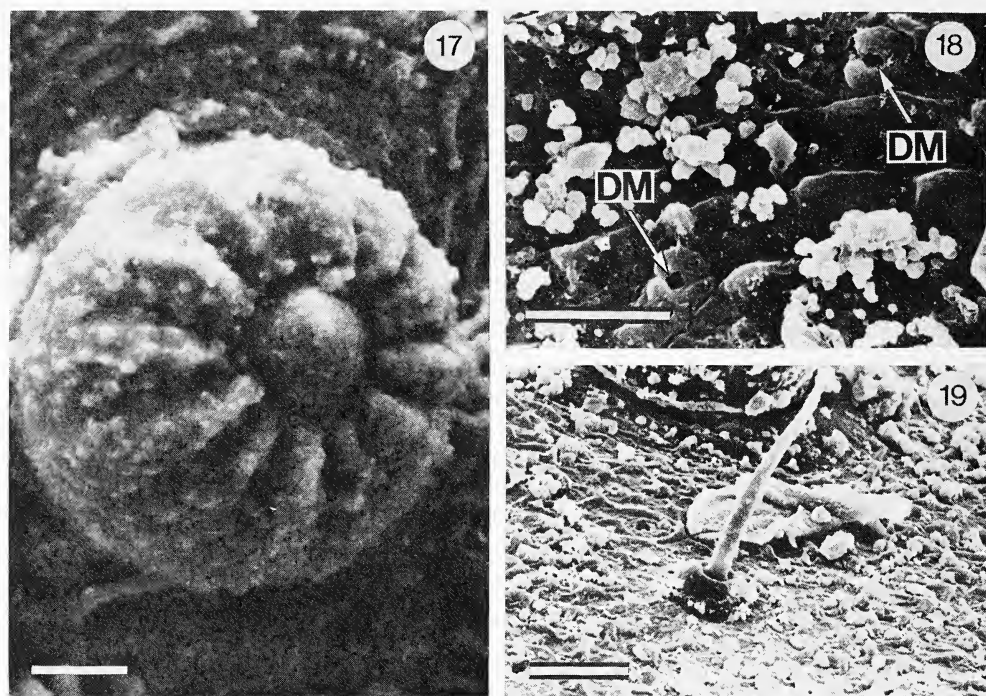
many closely associated papillae range from 50 to 65 μm in diameter and appear in transverse rows across the dorsum (Fig. 14). For the time being, I term these structures "cycloid facetodea" since they resemble the multifaceted compound eyes of insects.

Abdominal setae: As illustrated in Fig. 15, the setae of *H. maculosus* closely resemble those of the two *Leiobunum* species.

***Eumesosoma nigrum* (Say).—Dorsal integument:** A pronounced tuberculate-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 16). The prominent tubercles are subspherical and constricted basally. The tubercles show radial symmetry above with abbreviated striae radiating from a rounded process (Fig. 17). The tubercles measure approximately 40 μm in diameter and 30 μm in height and no micropores are distinguishable above. The microgranulations are of variable size and appear as dentate projections of the integument. The basal width of the microgranulations ranges from 5 to 8 μm . Sparsely distributed micropores appear as microfoveolae and are partially encircled by incomplete microareolae (Fig. 18). The microareolae measure approximately 5 μm in diameter.

Abdominal setae: Arcuate-acicular, thick-shafted setae arise from concave depressions atop rounded microareolae (Fig. 19). The microareolae do not resemble the other cuticular features and range from 7 to 9 μm in diameter. The setae are spirally substriate.

***Odiellus pictus* (Wood).—Dorsal integument:** The cephalothoracic region of *O. pictus* exhibits a tuberculate-imbricate-reticulate morphology (Fig. 20). The



Figs. 17-19.—Opilionid dorsal integument morphology: *E. nigrum*; 17, tubercle; 18, dermal micropores (DM); 19, abdominal setae. Scale = 10 μ m.

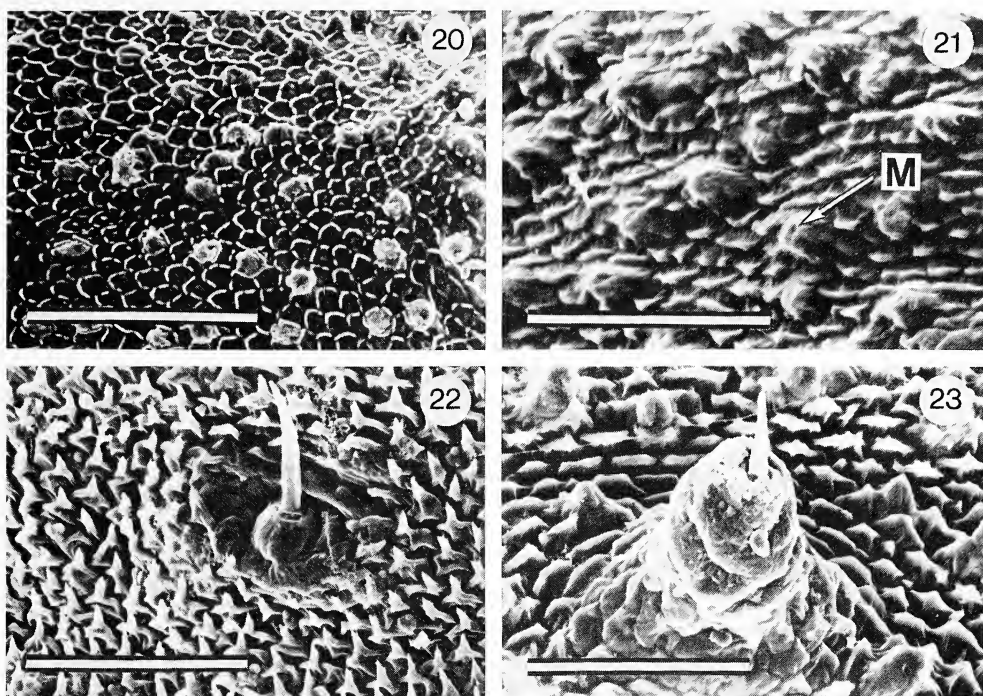
tubercles appear as rounded elevations of the integument, each possessing a micropore at its apex. Most of the tubercles are glabrous above but some are encircled by oblong laminae which are perpendicular to the cuticular surface. The imbrications are distributed as laminae and form a shingle-like arrangement. The distal margins of the laminae range from obtuse to acute. The reticulations appear as marginal elevations of the laminae.

A tuberculate-imbricate morphology is observed from the anterior abdominal region of this species (Fig. 21). The tubercles closely resemble those of the cephalothoracic region. However, the laminae are strongly keeled distally and occur in thickset layers. The distal margins of the laminae are acute.

The posterior abdominal region is imbricate-mucronate (Fig. 22). Tubercles are absent from the last two abdominal segments. The laminae occur in thickset layers and each ends in a fine point or mucro.

Abdominal setae: Two types of arcuate-acicular, thick-shafted setae are observed from the abdominal region. One form arises from external processes which are much larger than the abdominal tubercles, measuring approximately 40 μ m in height and 35 μ m in basal diameter (Fig. 23). The other type of setae arise from smaller tubercles measuring approximately 12 μ m in both height and basal diameter (Fig. 22). Each of these seta-bearing tubercles is located within an incomplete alveolus and is subparallel to the surface of the integument.

***Caddo agilis* Banks.—Dorsal integument:** A subimbricate-microtuberculate morphology is observed from the cephalothoracic region, particularly the ocularium of this species (Fig. 24). The surface of the integument has a subimbricate background of polygonal plates and microtubercles of variable size.



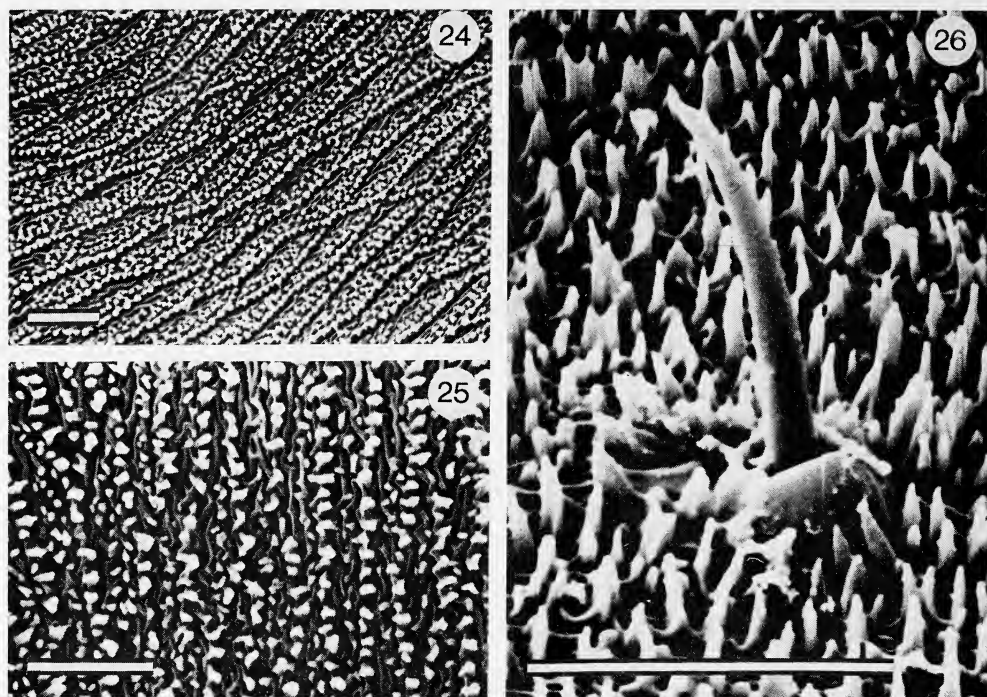
Figs. 20-23.—Opilionid dorsal integument morphology: *O. pictus*; 20, cephalothorax; 21, anterior abdomen showing micropore (M); 22, posterior abdomen and seta; 23, abdominal seta. Scale = 50 μm , except Fig. 20, 100 μm .

The larger microtubercles range from obtuse to subdeltoid and line the distal margins of the imbrications. Numerous smaller, obtuse microtubercles cover each of the polygonal imbrications. No micropores are observed from any region of the dorsum.

The abdominal region of *C. agilis* is rugose-plicate-microtuberculate (Fig. 25). The microstructure of the integument resembles that of the cephalothoracic region with the exception that the polygonal imbrications are not present. The cuticular surface exhibits a folded pattern of impressed striae in relief of torose plications. The microtubercles closely resemble those of the cephalothoracic region and project from the plications at irregular intervals. The integument of *C. agilis* is more easily distorted when desiccated prior to SEM than that of the other species examined.

Abdominal setae: Thick-shafted, arcuate-acicular setae arise from rectangular depressions atop microareolae (Fig. 26). The microareolae range from 7 to 9 μm in basal diameter and do not resemble other cuticular features. The setae are spirally substriate.

***Hesperonemastoma kepharti* (Crosby and Bishop).—Dorsal integument:** A microtuberculate-microgranulate morphology is observed from both the cephalothoracic and abdominal tergites of this species (Fig. 27). The numerous oblong, convex microtubercles exhibit microgranulations above and are constricted basally. A concave depression surrounds the posterior one-half of each microtubercle. The posterior margins of the microtubercles extend over the concave depressions and range from obtuse to acute. In the posterior abdominal



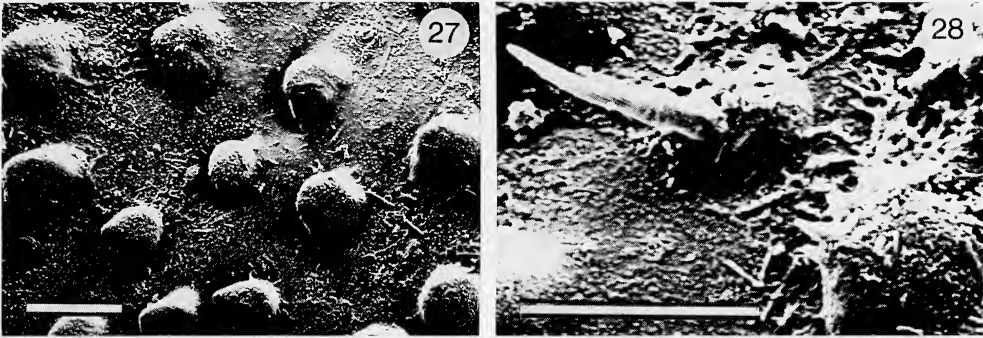
Figs. 24-26.—Opilionid dorsal integument morphology: *C. agilis*; 24, cephalothorax; 25, abdomen; 26, abdominal seta. Scale = 10 μ m.

region, some of the posterior tubercular margins exhibit a trident of acute microdenticles (Fig. 28). The microgranulations are of variable size and are often sparsely distributed upon primarily glabrous areas of the integument. No micropores are distinguishable from either the surfaces of the microtubercles or the microgranular background.

Abdominal setae: The setae are arcuate-acicular, spirally substrate, and thick-shafted (Fig. 28). They arise from the posterior margins of rounded microareolae at approximately a 45 degree angle to the integument.

DISCUSSION

Juberthie and Massoud (1976) conducted an SEM study of six cyphophthalmid species exclusive of *S. exilis* and reported that the species examined have similar cuticular features. The cuticular morphology of *S. exilis* closely resembles that of the six species studied by Juberthie and Massoud. Variations in cuticular morphology among the Sironidae include differences in the ratios of the two sizes of microgranulations per unit area, variations in the position of dermal gland micropores (e.g., a number of micropores are adjacent to the tubercles in *Metasiro americanus* (Davis)), and differences in the shape and size of the tubercles (Juberthie and Massoud 1976). This indicates that seven of the more than 50 known cyphophthalmid species have the same basic cuticular morphology. Although Shear (1980) did not use cuticular morphology as a taxonomic character in his reclassification of the Cyphophthalmi, further studies of representatives of the related family Pettalidae and superfamilies Stylocelloidea



Figs. 27-28.—Opilionid dorsal integument morphology: *H. kepharti*; 27, dorsum; 28, abdominal seta. Scale = 10 μ m.

and Ogoveoidea are needed to determine the importance of integumental microstructure in classifying cyphophthalmids.

The cuticular morphology of *V. sayi* most closely resembles that of *Erebomaster* sp., although these species are only distantly related. A rivulose-microgranulate cuticular microstructure and a horizontal setal position are exhibited by both species. However, *Erebomaster* sp. exhibits neither an imbricate morphology nor any apparent micropores. The tubercles of *V. sayi* differ in shape and number from those of *Erebomaster* sp. A morphological gradient exists in the cuticular features of *V. sayi* which is illustrated by the progression from cephalothoracic tubercles to abdominal imbrications.

Eisner et al. (1971) reported leg dabbing as a defensive measure of *V. sayi*. This may indicate that the cuticle of this species does not function in dispersing defensive secretions since these chemicals are actively applied to the potential predator rather than diffusely disseminated over the dorsal integument to form a "chemical shield". A chemical shield is produced by the laniatorid *Stygnomma spinifera* (Packard) whose repellent secretions flow along lateral grooves of its dorsum, possibly by capillary action, before spreading over the dorsum (Duffield et al. 1981). The author has observed similar lateral grooves in an undetermined species of the Phalangodidae. No lateral grooves were observed on *Erebomaster* sp. in the present study. Although no live material was available for observations of the defensive behavior of *Erebomaster* sp., ventral grooves below the scent glands and hirsute segments of tarsi I are present. These leg dabbing characters are similar to those illustrated by Eisner et al. (1977) for two neotropical species of the Cosmetidae.

The cuticular morphology of *L. vittatum* to a great extent resembles that of its congener, *L. holtae*, and the confamilial *H. maculosus*. The dorsum of *L. vittatum* exhibits transverse and lateral bands which are devoid of tubercles and which were not observed in the other opilionids examined. Martens (1978) made reference to lateral "Kanalen" or channels on the surface of the opilionid integument which may function in dispersing the secretion of the scent glands. The transverse and lateral bands observed in *L. vittatum* may function in dispersing its copious scent gland secretion. The size and morphology of the setae of *L. vittatum* are with few exceptions similar to those of *L. holtae*, *H. maculosus*, *E. nigrum*, *C. agilis*, and *H. kepharti*. Spicer (1987) illustrated a type of palpal mechanoreceptor (sensilla chaetica) from *Leiobunum townsendi* Weed that

exhibits "whorled striae". Apparently, both sensory and non-sensory setae exhibit the spirally substriate morphology in *Leiobunum*, although additional species should be examined.

Only the absence of microgranulate transverse and lateral bands distinguishes *L. holtae* from *L. vittatum* in terms of cuticular morphology. Also, only the absence of denticles and cycloid facetodea may be used to distinguish *L. vittatum* and *L. holtae* from *H. maculosus*. Although various types of cycloid facetodea were observed in *V. sayi*, *Erebomaster* sp., *O. pictus*, and *C. agilis*, only those of *H. maculosus* are illustrated since they distinguish this species from *L. vittatum* and *L. holtae* in terms of cuticular microstructure. The function of these possibly glandular structures is unknown and histological studies are needed.

The cuticular morphology of *E. nigrum* is interesting because of the characteristic form of the tubercles. Cokendolpher (1980) referred to "obtuse tubercles scattered over the entire dorsum" in descriptions of the six species of *Eumesosoma*. The tubercular micropores observed in *L. vittatum*, *L. holtae*, *H. maculosus*, and *O. pictus* are not present in the confamilial *E. nigrum*. The setae of *E. nigrum* are similar in both size and structure to those of *L. vittatum*, *L. holtae*, *H. maculosus*, *C. agilis*, and *H. kepharti* but differ in that they are emitted from concave depressions atop the microareolae.

The microstructure of the integument of *O. pictus* is distinct because of its prominent laminar imbrications which cover the dorsum. The diversity in form of the laminae from the different cuticular regions of *O. pictus* demonstrates a morphological gradient. The tubercles of *O. pictus* resemble those of the confamilial *L. vittatum*, *L. holtae*, and *H. maculosus* since they exhibit micropores, but differ in that they generally are not covered by laminae.

The cuticular morphology of *C. agilis* is striking because of the numerous subdeltoid microtubercles and rugose abdominal integument. The imbricate morphology of the cephalothoracic region of *C. agilis* is in some respects similar to that of *O. pictus*, although these species are not closely related. The laminae of *C. agilis* are less prominent than those of *O. pictus* and are only seen in one area of its dorsum while in *O. pictus* they cover all regions. The diversity in the pattern of the microtubercles of *C. agilis* demonstrates a morphological gradient for this species. Shear (1975) described the dorsal cuticle of *C. agilis* as "soft and leathery without tubercles, spines, or prominent setae" in his taxonomic treatment of the Caddidae. Gruber (1974) referred to a soft cuticle with a finely granular, regularly arranged surface for *C. agilis*. The less sclerotized cuticle of *C. agilis* may, with further studies, be linked to the fact that this species is restricted to very humid, densely shaded habitats.

The cuticular morphology of *H. kepharti* is distinct because of the posteriorly oriented microtubercles and the relatively unornamented cuticular background. The setae of *H. kepharti* are similar to those of *L. vittatum*, *L. holtae*, *H. maculosus*, *E. nigrum*, and *C. agilis* but differ in that they are emitted from posterior microareolar margins at a 45 degree angle. Gruber (1970) does not specifically refer to the characteristic microtubercles of *H. kepharti* in his redescription of the species. Grainge and Pearson (1966) described a different cuticular morphology exhibiting numerous closely and regularly packed laminae in the related European species *Nemastoma lugubre* (Muller). Shear (1986) described and illustrated both the dorsal and ventral cuticular morphology of *Crosbycus dasycnemus* (Crosby) which he placed closest to *Hesperonemastoma* in

his cladistic analysis of the Ceratolasmatidae. The numerous microtubercles (denticles) of the dorsal integument of *C. dasycnemus* resemble those of *H. kepharti* but were not illustrated at sufficient magnification for a detailed comparison. Shear also reported the presence of tridentate "scales" or cuticular processes on the ventral surface of *C. dasycnemus* which represents a marked difference in dorsal and ventral cuticular morphology. Although no descriptions of the ventral integument are given for the species in the present study, few differences in dorsal and ventral morphology were observed in specimens whose venters were examined, including that of *H. kepharti*.

Few descriptions of the function(s) of the opilionid integument have been reported other than its physiological ability to resist desiccation (Edgar 1971) and its role in dispersing scent gland secretions discussed above. Martens (1978) indicated that the integuments of representatives of the Trogulidae, Dicranolasmatidae, and Sclerosomatinae are strikingly glandular-papillose and that soil particles adhere to the secretions of these glands producing camouflage. It is hoped that future studies will discover still other properties and functions of the opilionid integument and its secretions.

Only in recent years have taxonomic studies of opilionids included cuticular morphology as a character for analysis. Variations in integumental microstructure among families, genera, and species were used by Shear (1983, 1986) as characters for cladistic analysis. From the present study it is evident that the cuticular morphology of opilionids is a reliable character as long as adult specimens are examined, and may be used in addition to more traditional characters in systematic studies. I believe that the surface of the opilionid integument, just as Cooke and Shadab (1973) predicted for the ricinuleids, may possess a "considerable but largely untapped systematic potential."

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APPENDIX 1

Systematic list of the species included in this study. *=This species was determined to be near *Erebomaster acanthina* (Crosby and Bishop) but sufficiently distinct for new species status by Thomas S. Briggs of San Francisco, California.

Suborder Cyphophthalmi

Superfamily Sironoidea

Family Sironidae

Siro exilis Hoffman

Suborder Laniatores

Superfamily Gonyleptoidea

Family Cosmetidae

Vonones sayi (Simon)

- Superfamily Travunoidea
 - Family Cladonychiidae
 - Erebomaster* sp.*
 - Suborder Palpatores
 - Superfamily Phalangioidea
 - Family Phalangiidae
 - Subfamily Leiobuninae
 - Leiobunum vittatum* (Say)
 - Leiobunum holtae* McGhee
 - Hadrobunus maculosus* (Wood)
 - Eumesosoma nigrum* (Say)
 - Subfamily Oligolophinae
 - Odiellus pictus* (Wood)
 - Superfamily Caddoidea
 - Family Caddidae
 - Caddo agilis* Banks
 - Superfamily Ischyropsalidoidea
 - Family Ceratolasmatidae
 - Hesperonemastoma kepharti* (Crosby and Bishop)
-

APPENDIX 2

Glossary of proposed morphological terms for describing the opilionid integument.

-
- Acicular*: needle-shaped; with a long, slender point as in certain setae.
 - Acute*: sharply pointed; refers to laminar margins or other cuticular processes.
 - Alveolus*, pl. *alveolae*: a small depressed or cup-like cavity; refers to setal insertions or sockets.
 - Arcuate*: arched; setae that are curved like a bow.
 - Areole*, pl. *areolae*: a pore-like depression; refers to insertions of certain setae within rounded microtubercles.
 - Deltoid*: elongate-triangular as in certain cuticular processes; resembling the Greek letter delta with its apex extended.
 - Dentate*: toothed, with tooth-like prominences.
 - Denticle*: a tooth-like prominence; a general term.
 - Facetodea*: cuticular structures composed of numerous small facets.
 - Foveolus*, pl. *foveolae*: a minute pit or micropore.
 - Glabrous*: smooth; devoid of any surface features.
 - Granulate*: surfaces composed of small, obtuse to acute granules.
 - Imbricate*: cuticular laminae that partially overlap as in roof shingles or fish scales.
 - Lamina*, pl. *laminae*: cuticular layers, plates or scales that are generally imbricate.
 - Micro-*: precedes terms describing features that measure 0.01 mm or less in size.
 - Mucronate*: terminating in sharply pointed processes as in the margins of certain laminae.
 - Obtuse*: blunt or rounded as opposed to sharply pointed.
 - Plicate*: folded; impressed with striae to produce the appearance of having been folded or pleated.
 - Punctate*: possessing circular, concave punctures or regular depressions.
 - Punctulate*: finely punctate; with numerous small and closely set punctures or micropores.
 - Reticulate*: superficially net-like or made up of a network of elevated, angular ridges; with surface ornamentation forming polygonal areas.
 - Rectilinear*: in the form of a straight line as in certain setae.
 - Rivulose*: exhibiting small, sinuate furrows or rivulets which are not parallel.
 - Rugose*: wrinkled; refers to a pattern of impressed, irregular striae which are both parallel and intersecting producing a wrinkled appearance.
 - Sinuate*: consisting of small sinuses; refers to wavy furrows of the integument.
 - Striae*: narrow impressed lines or furrows of the integument which may be parallel or intersecting.
 - Sub-*: below; somewhat; slightly; to a lesser degree than the term it precedes.
 - Torose*: swollen; possessing superficial swellings or protuberances.
 - Tuberculate*: exhibiting rounded, projecting protuberances which may possess a micropore.
-

RESEARCH NOTES

***ZELOTES SANTOS* (GNAPHOSIDAE, ARANEAE): DESCRIPTION OF THE MALE FROM SIERRA DE LA LAGUNA, B.C.S., MEXICO**

The species *Zelote santos* was described by Platnick and Shadab in 1983, being included in the *catholicus* subgroup, with only female specimens. In this paper I describe the male of *Z. santos* collected in the oak-pine forest at Sierra de la Laguna, B.C.S.

Zelotes santos Platnick and Shadab
Figs. 1-2

Two males were collected at an elevation of 1640 m in the oak-pine forest litter of Sierra de la Laguna B.C.S., Mexico, 5 March 1987 (F. Cota, A. Cota), 21

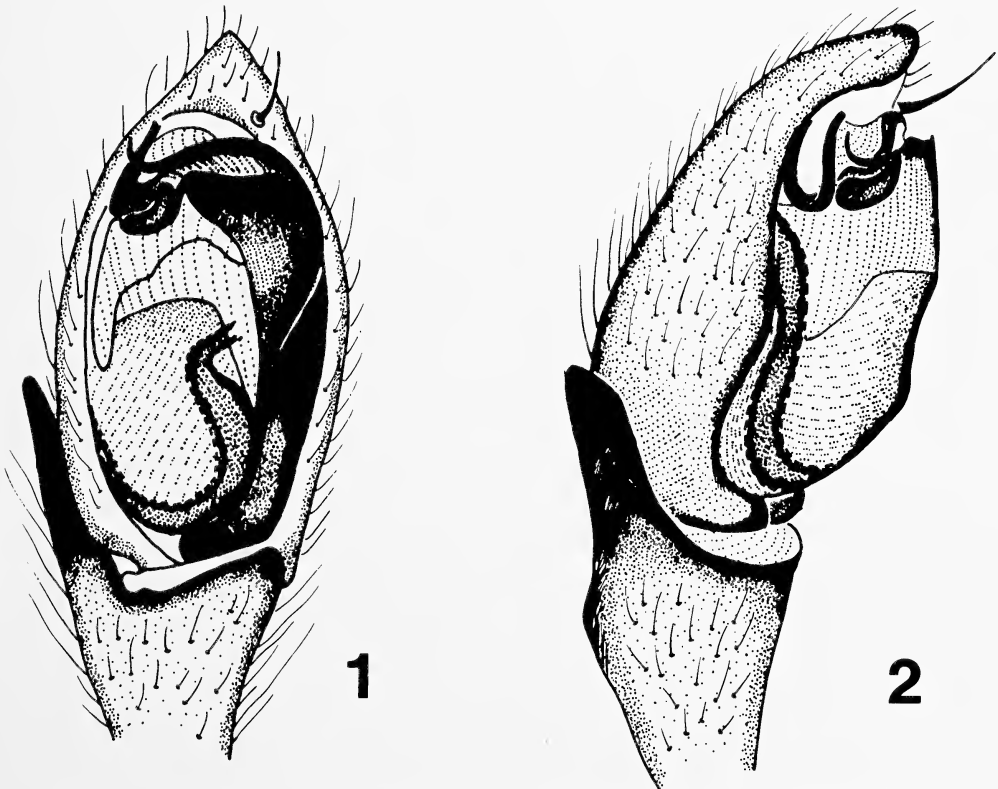


Fig. 1-2.—*Zelotes santos* Platnick and Shadab, male palp: 1, ventral view; 2, lateral view.

August 1987 (M. Vazquez). Specimens are deposited at the Arachnological Collection of the Centro de Investigaciones Biologicas de Baja California, Sur.

Description.—*Male*: Total length 6.0-6.3 mm; carapace 2.6-2.8 mm long, 2.0-2.2 mm wide (two specimens measured). Carapace dark brown with black reticulations and bright, with long black setae, thoracic groove longitudinal; anterior eye row recurved, posterior eye row straight, diameters and interdistances: AME 0.05-0.06, ALE 0.08-0.10, PME 0.06, PLE 0.08; AME-AME 0.05-0.06, AME-ALE 0.02, PME-PME 0.07, PME-PLE 0.03, ALE-PLE 0.06-0.08; MOQ length 0.20, front width 0.35, back width 0.45; chelicerae dark brown, retromargin of fang furrow with two teeth, and promargin with four; sternum with marginal brush of setae and sclerotized extensions to and between coxae. Legs dark brown with tarsi lightest, distal halves of metatarsi and tarsi scopulate; femur I 2.25 mm long with 2 dorsal macrosetae, 1 prolateral; tibia I 2.0-2.1 mm long with 0 macrosetae; basitarsus I 1.55-1.75 mm with 2 proventral macrosetae, tibia III 1.1-1.2 mm with one prodorsal macroseta; 3 internolaterals, 3 externolaterals, and three pairs of ventral macrosetae. Opisthosoma dark gray with shiny brown scutum, venter light yellow, spinnerets light. Palp with terminal apophysis narrow and long, fused dorsally to embolar base, bearing a curved projection and curved embolus without prolateral hump; intercalary sclerite apparently fused with subtegulum (Figs. 1-2).

Diagnosis.—*Male*: *Zelotes santos* seems closest to *Z. union* in having a low embolus, but can be distinguished by the much longer terminal apophysis.

Range.—Known only from the male locality.

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TRANSITION FROM PREDATORY JUVENILE MALE TO MATE-SEARCHING ADULT IN THE ORB-WEAVING SPIDER *NEPHILA CLAVIPES* (ARANEAE, ARANEIDAE)

Behavioral strategies of male orb-weaving spiders change rather dramatically as they mature to adulthood. Juvenile males are sedentary predators, capturing prey on webs of their own construction. However, upon reaching adulthood, they shift to a search strategy, approaching females who usually inhabit solitary webs

(Robinson 1982). As pronounced as these changes are, few field data have been gathered on marked, unrestrained juvenile males as they mature to adulthood. The purpose of this study is to provide ethological descriptions of this transition phase in the life cycle of *Nephila clavipes*, a New World orb-weaver. Specifically, we describe web maintenance, changes in body coloration and size, sperm web construction, sperm transfer to the palps, and dispersal as males mature from the penultimate instar to adulthood.

Forty-one juvenile males in the penultimate instar were observed from the second week in July to the last week in August, 1984 at the F. Edward Herbert Center of Tulane University, located about 20 km south of New Orleans, Louisiana. Criteria for inclusion were that the male must have been residing on a male-constructed web, and there had to be evidence of the final molt during the course of observation. These criteria were met by 28 males.

A census of the males was taken every morning between 0800 and 1000 h. For individual identification, each was marked on the dorsum of the abdomen with fast-drying acrylic paint. Data collected include: estimated amount of viscid spiral in good repair, number of sperm webs, abdominal coloration, and occurrence of molt. The day of the molt was determined by the absence of a paint mark on a recently molted male inhabiting an identified web and/or the presence of a paint-marked exoskeleton. Subjects were re-marked after molting and checked daily until they abandoned the web. The adjacent forest area was searched daily for marked males.

To quantify the change in size occurring at the final molt, we examined eight unrestrained, unmarked males found outside of the census area who had just molted to adulthood. The exoskeleton as well as a front leg (I) were removed and the tibia-patella length of the leg and corresponding portion of the exoskeleton was measured (following Vollrath 1983). For comparison, legs and exoskeletons of 17 females maturing to adulthood were measured in a similar manner.

By the day of the final molt, males had allowed their viscid spirals to almost totally deteriorate (Table 1), as do females at the final molt (Christenson et al. 1985). However, males did not construct a stabilimentum on the final web, as do females (Robinson and Robinson 1973).

The length of the tibia-patella portion of the male front leg increased by 21.5% (SD = 8.8) from the penultimate to the final instar. This was significantly less than the rate of growth for maturing females (35.8%, SD 10.2; $F = 11.445$, df 1,23, $p = 0.003$).

Males built their first sperm web an average of 2.1 days (SD = 0.55) after molting. The typical sperm web was trapezoidal, about 5×5 mm in size, and located in the barrier strands or remains of the viscid spiral. Two males were observed constructing sperm webs. First, they moved the abdomen back and forth between what appeared to be already established silk strands, for 150 s in one case and 270 s in the other. To the unaided eye, the resulting web appeared as a dense mat of fine strands. The genital opening was then moved against the web with one male bouncing and the other pushing the ventral abdomen onto the web. Sperm deposition took 75 and 60 seconds. Very quickly thereafter the males began dipping the palps onto the web with the conductor held parallel to the web plane. They were dipped in a mostly alternating manner, once every two seconds, for 105 and 135 seconds. Microscopic examination of ten sperm webs revealed

Table 1.—Census data relating to condition of the viscid spiral and presence of sperm webs on the orbs of male *N. clavipes* gathered during a ten day period around the time of their final molt.

| Day | <i>N</i> | % of Viscid Spiral Intact | | % of Orbs with Sperm Webs | Of Orbs with Sperm Webs, <i>X</i> Number Present | Range of Sperm Webs |
|-----------|----------|------------------------------|------|---------------------------------|---|------------------------|
| | | >90% | <10% | | | |
| PRE-MOLT | | | | | | |
| 5 | 17 | 0.94 | 0.06 | 0 | — | — |
| 4 | 19 | 0.89 | 0.11 | 0 | — | — |
| 3 | 21 | 0.52 | 0.34 | 0 | — | — |
| 2 | 25 | 0.40 | 0.36 | 0 | — | — |
| 1 | 25 | 0.12 | 0.79 | 0 | — | — |
| Molt | 28 | 0.04 | 0.93 | 0 | — | — |
| POST-MOLT | | | | | | |
| 1 | 25 | 0.00 | 1.0 | 12.0 | 1.0 | 1-1 |
| 2 | 19 | 0.00 | 1.0 | 68.4 | 2.2 | 1-5 |
| 3 | 8 | 0.00 | 1.0 | 75.0 | 1.5 | 1-2 |
| 4 | 3 | 0.00 | 1.0 | 100.0 | 2.0 | 1-3 |

the strands to be loose and tangled in appearance. Transfer to the palps must be quite efficient because only one web contained sperm, and it had only one sperm.

Frequently, we found several sperm webs on a given orb (Table 1). Unfortunately, it was not possible to accurately determine the total number of sperm webs constructed by a given male. They were damaged by wind and rain and thus nearly impossible to individually recognize from day to day.

During this time male color is changing. Typical abdomen coloration of the juvenile male was female-like, yellow/caramel and white (see Levi 1980). In the penultimate instar, palps and femurs were a translucent light grey. However, on the day after the final molt, abdomen coloration was darker for half of the subjects, palps darker in all males, and femurs darker in 86%. By the third day, 20% of the males had the typical adult abdominal coloration, a uniform dark caramel or copper. The black midline stripe and the black elongated marks lateral to posterior abdomen, prominent in juveniles, were visible but relatively faint. Adult coloration was complete in about one week. These color changes were more pronounced than those of the female, for they maintain the yellow juvenile coloration.

Robinson and Robinson (1976) noted that the functions of maturational color changes are not clear. It is possible that the relatively dark color of the male serves as camouflage while moving on branches or twigs when between female webs. Predatory pressure on moving males is thought to be relatively high (Christenson & Goist 1979; Vollrath 1980). Whatever their significances, changes in coloration are indispensable in estimating male age.

Males abandoned the web an average of three days (SD = 0.74) after molting and an average of one day (SD = 0.74) after appearance of the first sperm web. Eight of our 28 males were found on female webs, six with a juvenile female and two with a female who had just molted. It should be noted that most females in the immediate area were juveniles. Only one male had moved to the nearest female; their webs were already connected.

Although mating occurs on the female's web, sperm webs are infrequently found there. In July, out of a total of 770 census-days of marked males on female

webs, only seven sperm webs were noted. Census data gathered in a similar manner in 1982 indicated 17 sperm webs on female orbs in a total of 628 marked male-days. In three of these cases, the male present did not yet have the adult coloration and probably had not had the opportunity to build sperm webs on its own orb prior to abandonment. The failure of sperm webs to appear after mating is consistent with the observation that male *N. clavipes* deplete their sperms stores after mating with a female just after her final molt and do not produce more sperm (Manuscript in preparation).

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MALE RESIDENCY ON JUVENILE FEMALE *NEPHILA CLAVIPES* (ARANEAE, ARANEIDAE) WEBS

Male orb-weaving *Nephila clavipes* leave their own individually-constructed orbs after the final molt and move about in search of mates. Males are likely to land on webs of females of various instars for it appears that they are not attracted to webs of sexually receptive females by distance-acting pheromones (Christenson et al. 1985). Once on the female's web, duration of male residency might be related to female instar because adult males are often found on webs of

larger than smaller juvenile females (Farr 1976; Brown et al. 1985). First, we asked if marked, unrestrained male *N. clavipes* remain longer on a web inhabited by a female in the penultimate instar, approaching sexual receptivity, than on a web of a relatively smaller juvenile, three or four instars from adulthood. We found that they do remain longer with the female in the penultimate instar.

Female responsiveness could be one factor underlying this variation in male residency. If so, one would expect juvenile females of different instars to respond differently to adult males. Second, we placed males onto juvenile female webs to determine if females in the penultimate instar respond less aggressively than females in earlier instars.

Observations were conducted at the F. Edward Herbert Center of Tulane University, located about 20 km south of New Orleans, Louisiana. To determine if duration of male residency on the web is affected by female instar, we examined census data gathered during July and August, 1980 and 1982 on paint-marked males, small juvenile females (12-15.5 mm in cephalothorax-abdomen length), and females in the penultimate instar (18-23 mm). Females in the latter group were observed to molt once and mate. To ensure that the duration of male residency was most likely determined by the subject male, we analyzed only those cases ($N = 36$) in which the female remained on the web after the male had departed and in which no other male had come onto the web, possibly displacing the male in question.

Female response to an added male was observed during the mating season, from July to mid-August, 1980. Juvenile males in the penultimate instar were placed in Fiberglas-screened enclosures situated in the field and fed *Drosophila* daily. No sooner than four days after their final molt, twenty males were paint-marked and randomly assigned to a relatively small juvenile female (12-14 mm) or a female in the penultimate instar (18-20 mm). Other males already present on the females' webs were removed and the subject males were transported on a thin stick and gently placed on barrier strands, about 30 cm from the hub. Male and female behaviors listed in Table 1 were recorded serially for 20 minutes. Three males placed with small juveniles moved onto adjacent foliage within the first minute. In two cases this occurred before the female had made any behavioral response. In the other case the female response, one pluck, did not immediately precede the male's departure. A fourth male spent most of the observation period under a leaf at a silk attachment point. Data for these four males were excluded from statistical analyses.

Analysis of census data revealed that marked, unrestrained males remained an average of 2.6 days ($SD = 2.6$) with small juvenile females whereas males remained 9.1 days ($SD = 5.2$) with females in the penultimate instar ($F = 17.84$, $df = 1,34$, $p = 0.0001$).

After the male was added to the web, large and small juvenile females strand-plucked while at the hub with about equal frequency (Table 1). However, the small females oriented to the male, strand-plucked while oriented, and chased the male more frequently (Table 1). Males slowly approached while probing both sizes of females with about equal frequency. Males with larger females spent more time within 10 cm of the female ($x = 620.2$ s versus $x = 242.5$ s; $F = 5.343$, $df 1,14$, $p = 0.002$), abdomen vibrated and probed while stationary more frequently (Table 1), and, by the end of the 20 minute observation period, were more likely to be within 10 cm of the hub (9/10 LG, 3/7 SM; Chi Square = 4.41, $p = 0.036$) than the males with smaller females. Most of the males of both groups remained for at

Table 1.—Behavior of small juvenile *N. clavipes* females (12-14 mm) and larger juvenile females in the penultimate instar (18-20 mm) and the adult males placed on webs of these females during a 20 minute serial record. a = multiple occurrences without a return to hub position were scored as one event; b = each pluck scored as a separate event; c = often occurring repeatedly in a prolonged sequence which was scored as one event; intermittent sequences separated by 5 s were scored as multiple events; d = bouts of rapid vibration of the posterior tip of the abdomen; and e = a sweeping, waving of the l's while stationary in barrier strands.

| | Small Juvenile (n=6) | | Large Juvenile (n=10) | | F | P |
|--|----------------------|------|-----------------------|------|-------|-------|
| | x | SD | x | SD | | |
| FEMALE BEHAVIOR | | | | | | |
| Orient to male ^a | 8.5 | 5.8 | 4.0 | 2.9 | 4.261 | 0.058 |
| Strand-pluck in hub position ^b | 4.7 | 2.3 | 5.5 | 5.5 | 0.120 | 0.734 |
| Pluck while oriented to male ^b | 14.2 | 12.1 | 5.0 | 4.4 | 4.854 | 0.045 |
| Approach male ^a | 3.3 | 4.1 | 0.9 | 1.4 | 3.101 | 0.100 |
| Chase male ^a | 1.3 | 1.4 | 0.2 | 0.6 | 5.214 | 0.039 |
| MALE BEHAVIOR | | | | | | |
| Slow approach and probe ^c | 38.3 | 22.9 | 38.5 | 19.1 | 0.001 | 0.988 |
| Probe with l's while stationary ^c | 9.7 | 9.7 | 63.6 | 52.9 | 5.943 | 0.029 |
| Abdominal vibration ^{c,d} | 0.3 | 0.8 | 16.2 | 14.4 | 7.118 | 0.018 |
| Lateral leg sweeps ^{c,e} | 2.7 | 4.8 | 1.9 | 1.8 | 0.211 | 0.653 |

least 24 hours (6/9 S, 8/9 L). This does not necessarily exclude female responsiveness as a factor contributing to duration of residency. Census data show that males on the webs of smaller females remained, on the average, two and one half days. Duration of male residency beyond the first day was difficult to assess for the added males because some females abandoned the web before the male did or a larger male came onto the web, possibly displacing the subject male.

We conclude that unrestrained males spend relatively more time on the web of a female approaching her final molt, which is probably adaptive for the male. We suggest that female response to the male might be one factor underlying this variation in male residency.

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NATURAL HISTORY OBSERVATIONS OF *SALTICUS AUSTINENSIS* (ARANEAE, SALTICIDAE) IN NORTH-CENTRAL TEXAS

The zebra spider, *Salticus austinensis* Gertsch, is a small jumping spider reported only from Texas. In north-central Texas it is widely distributed and in suitable habitats may reach high population densities. The localized density of this zebra spider as well as its diurnal habits, preference for open, exposed foraging grounds, and conspicuously bold black-and-white markings, makes it an ideal subject for field behavioral studies. Although some behavioral investigations into the closely-related *S. scenicus* (Clerck) are available (Jacques and Dill 1980, Am. Nat. 116:899-901), no such information exists for *S. austinensis*.

A population of *Salticus austinensis* inhabiting the outside walls of a brick veneer home in Wichita Falls, Texas, constituted our original sample. Observations of the spiders' activities from April through July 1986 were recorded on an almost daily basis for periods varying from ten minutes to four hours. A captive population of 18 adult zebra spiders (2 males, 16 females) was maintained in a single cage measuring 40 × 20 × 25 cm for further observations and collection of reproductive data. Field observations were conducted in Archer, Baylor, Clay, and Wichita counties of north-central Texas. The following generalizations regarding aspects of the natural history of *S. austinensis* are based on our observations under both natural and controlled situations.

Periods of activity.—Zebra spiders exhibited more restricted periods of active foraging than other species of sympatric hunting spiders (i.e., *Phidippus audax*, *Metacryba taenolia*, *Platycryptus undatus* and *Metaphidippus* imm.) and were usually the last to appear and first to retire. Although we have sightings from shortly after sunrise to one hour before sundown, most sightings were during the hours of maximum light from ca 1000 h to 1500 h. Since *Salticus*, like many species of spiders, is not a daily forager, the maximum number of sighted adult individuals at our original site fluctuated considerably.

Temperatures during our period of observations ranged from near 22° to 40°C, and seemed to have no major effect on spider activity. However, overcast and rainy days resulted in noticeably lessened activity. Winds seemed to curtail foraging on some days, especially when gusts exceeded 32 kmp.

Distribution and habitat.—Carpenter (1972, Southwestern Nat. 17(2):161-168) noted that the zebra spider in Wichita County was restricted largely to vertical surfaces such as tree trunks and walls of buildings. Throughout our study area, we found this to be true, although overhanging surfaces of buildings and rock cliffs were equally suitable. Preferred foraging surfaces were relatively smooth, exposed, and well-lit, presumably to avoid ambush by predators.

Single spiders were occasionally noted foraging along tree trunks or collected by beating shrubs and trees. *Salticus austinensis* may well be widely distributed in sparse numbers at such sites. Greatly increased densities of *S. austinensis* (surpassing that of other spider species combined) was predictable in our study area where large areas of open foraging surfaces were available (e.g., walls of buildings, rock-faced cliffs, concrete dams), and wherever their preferred species of prey (midges) were abundant. Midges are aquatic breeders and occur in large populations near water. Foraging surfaces along shorelines of lakes, streams, and

large stock ponds, or surfaces farther from the water (but still within flight range of midges) that are illuminated at night and consequently attract midges, permit sizeable *Salticus* populations.

Prey species.—Forty-six prey items were randomly removed from feeding spiders. The majority of the prey were chironomid midges (74%). These were followed by mosquitoes (11%), small lepidoptera (9%), two small dipterans (4%) and a small beetle. The largest observed prey was a house fly. The chironomids comprised the majority of prey due to their abundance and their ease of capture.

Population biology.—Sex ratios heavily favored females. Males, readily characterized by their more slender build and elongate, dark chelicerae, never exceeded 10 percent of any observed population. Because of this sex bias, and because zebra spiders do not usually emerge daily, males often were not detected at observation sites.

Intraspecific interactions are characterized by mutual avoidance, although territorial displays between adult males were observed on two occasions. In the first such instance, the spiders met head-to-head with chelicerae and pedipalps oriented laterally at nearly a 180-degree angle for about five seconds before mutual retreat. The second encounter occurred within a small collecting vial in which two specimens were held. This interaction was only observed during the latter stage. One male assumed an immobile (and presumably submissive) posture while the second animal with fully extended chelicerae and pedipalps approached from the left side. Contact was maintained for several seconds before retreat by the aggressor. The two spiders remained indifferent to each other and were subsequently transferred into the population cage. Jacques and Dill (1980, Am. Nat. 116:899-901) record intraspecific encounters between *Salticus scenicus* but do not specify the sexes of their specimens.

We did not observe the hibernacula (webbed shelters) of *Salticus austinensis* under natural conditions, as they are apparently in available cracks and crevices in and around foraging grounds. A small crack in the overhang of our original study site was the entrance to overnight shelter for several adult spiders, which were noted to emerge from it, often within seconds of each other. Hibernacula of captive individuals appeared to be randomly dispersed in the population cage. Although there is no evidence that communal denning commonly occurs, we speculate that such may be the case in instances where suitable shelter for hibernacula is scarce. However, this would appear to be more a case of opportunistic behavior than of true sociality.

Reproductive potential of *Salticus austinensis* is low. Of seven egg clutches laid by captive specimens, the range of egg/clutch is two to five (mean, 3.6).

Interspecific relationships.—Zebra spiders carefully avoid all contact with other species of spiders, regardless of size. During foraging, zebra spiders carefully skirted webs of various sizes and species of theridiids. Observed predation by other spiders on *S. austinensis* was a rare event. A large *Phidippus audax* (Hentz) was observed feeding on an adult female zebra spider. On two occasions, adult female *Salticus* were observed in the webs of theridiids, one was dead and the other was still attempting to escape. These webs appeared abandoned, as they were vacated and cluttered with debris, and the trapping was apparently accidental.

Several mud-daubers, both *Sceliphron caementarium* (Drury) and *Chalybion californicum* (Saussure), were noted near some of our study sites, but

examination of the nests revealed oxyopids, thomisids, and a single *Platycryptus* to be the prey of these wasps.

At sites where *S. austinensis* was the most abundant species, the second most commonly found spider was the larger salticid, *Platycryptus undatus* (De Geer). The two species appear to occupy similar niches, although *P. undatus* often reside in exposed hibernacula and appear to be less active foragers. The two species exhibit mutual avoidance. On several occasions, the larger *Platycryptus* was attracted by the movement of a foraging zebra spider, but would never approach. We once confined adult females of each species together in a small plastic vial for 24 hours in an attempt to induce agonistic behavior, but none was observed.

In summary, some aspects of the population biology of the zebra spider, *Salticus austinensis*, appear unusual for the family Salticidae, and deserve further study:

- ecological and behavioral relationships among *Salticus* individuals and between *Salticus* and *Platycryptus undatus*;

- indicated low reproductive potential of this species, so conspicuous in markings and foraging behavior, and therefore presumably more prone to predation.

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FUNCTIONAL ASPECTS OF THE MALE PALPAL ORGAN IN *DOLOMEDES TENEBROSUS*, WITH NOTES ON THE MATING BEHAVIOR (ARANEAE, PISAUROIDAE)

In this note, we describe a locking mechanism in the male palp of *Dolomedes tenebrosus* Hentz, 1843, and include notes on mating behavior of the species.

In numerous spider families, the adult males possess a conspicuous tibial apophysis. These tibial apophyses occur in a great diversity of shape and form. They are often species-typical and frequently figured in taxonomic works to facilitate identification. Their function, however, is unknown. While observing the copulation of a pair of *D. tenebrosus*, we were able to preserve the male palp in the naturally expanded stage. The investigation of the palp provided an insight into the functional complex of the expanded genital bulb and tibial apophysis.

Thus far, the European *Dolomedes fimbriatus* (Clerck, 1758) is the only species of this large genus for which mating behavior and copulatory position are well known (Bonnet 1924; Gerhardt 1926). The male of *D. fimbriatus* displays a courtship consisting of rapidly waving his front legs and extending the pedipalps. The female postures in a specific position: all legs are held close to the body, and the patellae touch each other above the prosoma (Schmidt 1957). The male mates with the female on the ground or in the vegetation, using copulatory position II

(i.e., male on female's dorsum, facing in opposite direction, his prosoma over her abdomen), typical of the "modern hunting spiders" (Gerhardt 1924).

Only one copulation of *D. tenebrosus* was observed in the laboratory. The female (27 mm body length; collected Lynchburg, Virginia) had molted 14 days before, and the male (9 mm body length; collected Washington, D.C.) 72 days before the observation was made. The male was stimulated with silk threads made by the female, which were placed in his cage four hours prior to copulation. After dark the pair was placed on an arch formed of 25 mm wire mesh. The behavior was recorded on videotape with a Panasonic WV1854 video camera, using infrared light (> 800 nm wavelength). The female terminated the copulation by killing the male. We retrieved his body (with the right palp still expanded) and preserved it in 80% ethanol.

Courtship and copulation lasted 1.5 hours. The female was placed onto the wire screen, where she moved around for a few minutes and finally assumed a "ventral-up" position. The male was placed onto the wire screen at a distance of approximately 15 cm from the female. He waved with the outstretched front legs, contacted her silk lines, and approached the female. After the male had initially contacted the female and stroked her I and II legs, the female groomed these legs vigorously. During 50 minutes of courtship, the male lightly stroked and tapped the distal segments of the female's anterior legs and proceeded to stroke her abdomen. The female remained mostly motionless when contacted by the male.

The male climbed on the female's dorsum, their bodies parallel but pointing in opposite directions, as if anticipating copulatory position II. The female pulled her legs closer to the body; legs III and IV were not in contact with the wire screen. The male approached the female's venter from both sides, about 35 times in total. The female responded to each attempt by rocking her venter laterally toward the male, thus providing more room for the male to approach her epigynal area. This phase lasted for 32 minutes; tempo and frequency of the male's attempts increased during that time.

Copulation itself lasted about 4.5 minutes. The male abruptly passed completely across her right side and onto her venter in a perpendicular position, inserted his right palp into her right copulatory pore (Fig. 1), and simultaneously expanded the basal and median hematodochae. During the insertion of the palp, we observed no hematodochal pulsing. Both animals were still.

The female slowly pulled the male's body with her front legs into a parallel orientation to hers, juxtaposing his abdomen to her mouth. When the female bit the tip of the male's abdomen the palp sprang free of the epigynum almost immediately, and remained, in an expanded state, still attached to the male's body.

At this point we retrieved the male's body. A study of the expanded bulb revealed that a heavily sclerotized part of the embolic division fitted behind the tibial apophysis, and apparently arrested the rotation of the bulb. Figure 2 shows the expanded right palp in retrolateral view. The sclerites of the genital bulb are labelled according to Comstock's nomenclature (1910:180) used for *Dolomedes scriptus* Hentz, 1845. Attached to the distal end of the tegulum by an inflatable membrane is a strongly sclerotized tube. At its distal tip, this sclerotized tube bears the fulcrum, the lateral subterminal apophysis and the spiral embolus. During expansion, the membrane connecting the tegulum and the sclerotized tube is inflated and the sclerotized tube assumes an erect position. Due to the inflation

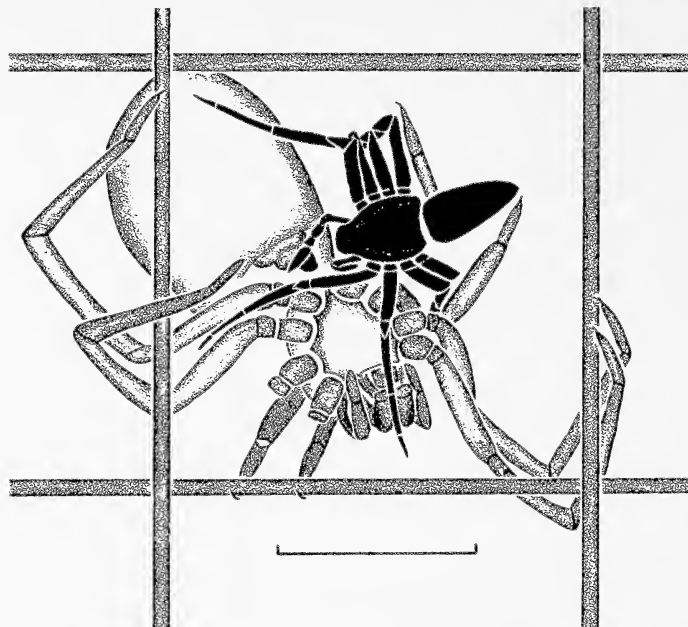


Fig. 1.—Copulatory position of *D. tenebrosus*, drawn from videotape. Male drawn in black. Scale = 1 cm.

and rotation of the basal and median hematodochae, the subtegulum-tegulum-complex is tilted towards the retrolateral side of the palp. In this position, the sclerotized tube fits snugly behind the tibial apophysis and arrests the rotation of the bulb. The described locking mechanism proved to be strong, and even repeated handling of the palp did not release the genital bulb from its arrested position.

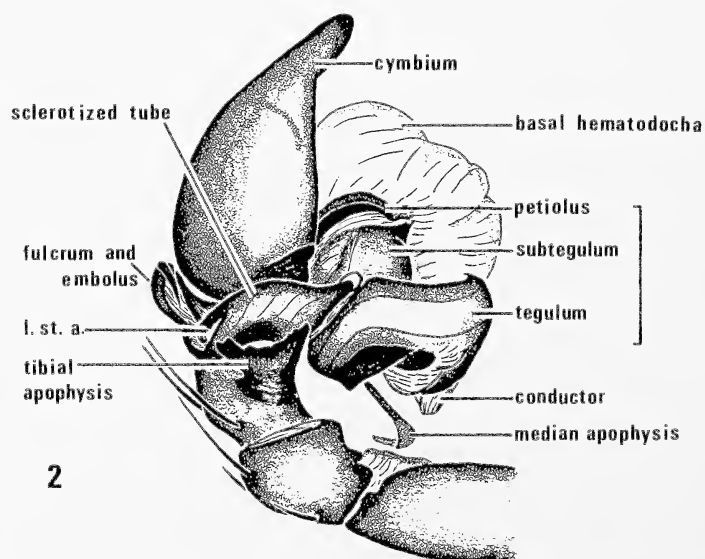


Fig. 2.—Dorsal view of expanded palp of *D. tenebrosus*. Bulb is "locked" behind tibial apophysis. l. st. a. = lateral subterminal apophysis. Scale = 1 mm.

The observation of an internal locking mechanism in the male palp during expansion sheds new light on the function of male tibial apophyses. Most genera currently assigned to the Pisauridae (or Pisauridae and Dolomedidae; Lehtinen 1967) possess well-developed and often large tibial apophyses. In many cases, they provide useful species-specific characters. Heimer (1982) described internal locking mechanisms in Theridiidae and Linyphiidae, in which the paracymbium and different parts of the bulb form a functional complex during copulation that arrests the rotation of the bulb. The locking mechanism in *D. tenebrosus* seems functionally similar although the structural elements of the mechanisms are not homologous.

The copulatory position of *D. tenebrosus* appears to be modified from the standard copulatory position II in *D. fimbriatus*, where the males are more similar in size to the females. The stroking motion of the male resembled the leg waving motion observed in *D. fimbriatus*, *D. scriptus*, *D. vittatus* Walckenaer, 1837, and *D. triton* (Walckenaer, 1837) (see Carico 1973; Roland & Rovner 1983). The female *D. tenebrosus* pulled her legs close to her body as if she were about to assume a posture similar to females of *D. fimbriatus*. *D. scriptus* and *D. vittatus* do not pull their legs close to the body while mating and the mating position is modified as well (Carico 1973).

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ANANTERIS FESTAE BORELLI, ESPECE DE SCORPION CARACTERISTIQUE DU CENTRE D'ENDEMISME "CHIMBORAZO" EN EQUATEUR

Dès sa création par Thorell, en 1891, le genre *Ananteris* s'est caractérisé par un nombre réduit d'espèces considérées comme très rares dans leur ensemble. Il est vrai que 62 ans se sont écoulés entre la description de la troisième espèce, *Ananteris cussinii* Borelli, 1910 et celle de la quatrième espèce, *Ananteris venezuelensis* Gonzalez-Sponga, 1972. Le travail de révision globale du genre (Lourenço, W. R., 1982, Bull. Mus. natn. Hist. nat., Paris, 4è sér., 4:119-151) apporte finalement une contribution plus large à la taxonomie et à la répartition géographique du groupe.

Aujourd'hui le nombre d'espèces connues d'*Ananteris* (15) s'est considérablement accru et même si plusieurs d'entre elles demeurent peu connues, d'autres constituent des cas d'endémisme assez nets.

Un exemple très intéressant de rareté d'une espèce est celui d'*Ananteris festae*, décrite par Borelli en 1899 sur un seul exemplaire femelle du Rio Peripá. Jusqu'à la révision du genre, cet exemplaire était le seul connu pour l'espèce. En 1982 deux autres exemplaires sont cités par Lourenço, un mâle et une femelle collectés à Rio Palenque, à 50 Km de Quevedo.

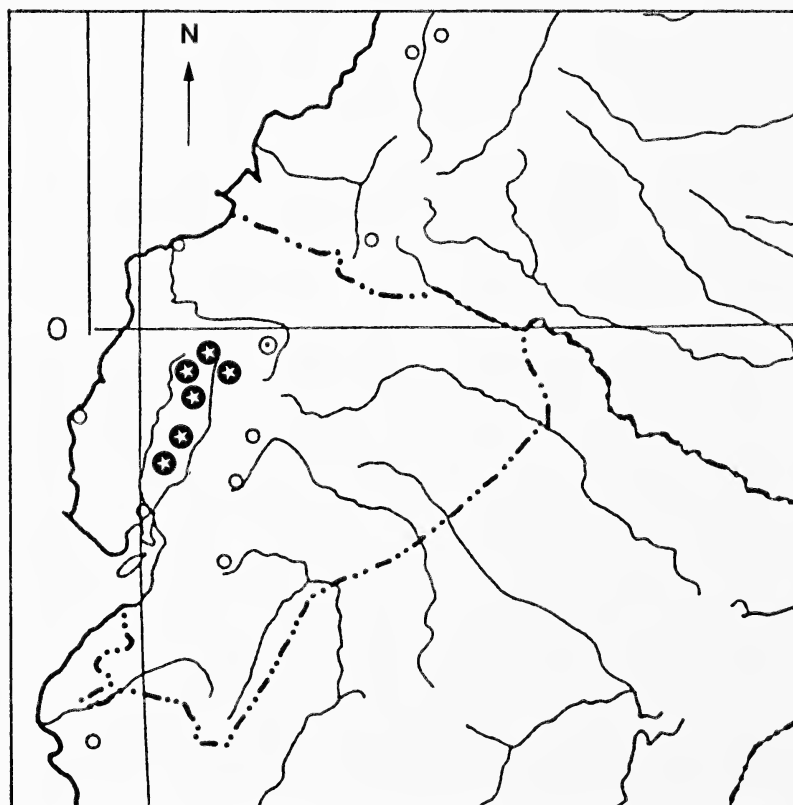


Fig. 1.—Répartition d'*Ananteris festae* en Equateur, en corrélation avec le centre d'endémisme "CHIMBORAZO".

La rareté d'une espèce comme *A. festae* qui habite un milieu forestier dans la litière est principalement due à deux facteurs: sa condition d'animal cryptique et sa petite taille; les mâles ne dépassent pas 15 mm et les femelles 20 mm. Ainsi toute chasse à vue n'est pas rentable.

A présent l'étude d'un plus grand nombre d'exemplaires collectés par des méthodes d'extraction de Berlèse permet de mieux connaître la répartition de cette espèce endémique pour le centre-ouest de l'Equateur (Fig. 1).

Ananteris festae présente une distribution endémique qui correspond très bien au centre d'endémisme "CHIMBORAZO" défini d'après l'étude des Papillons Heliconiini (Brown, K. S., 1979, Tese, Univ. Est. Campinas, Brésil, 265 p).

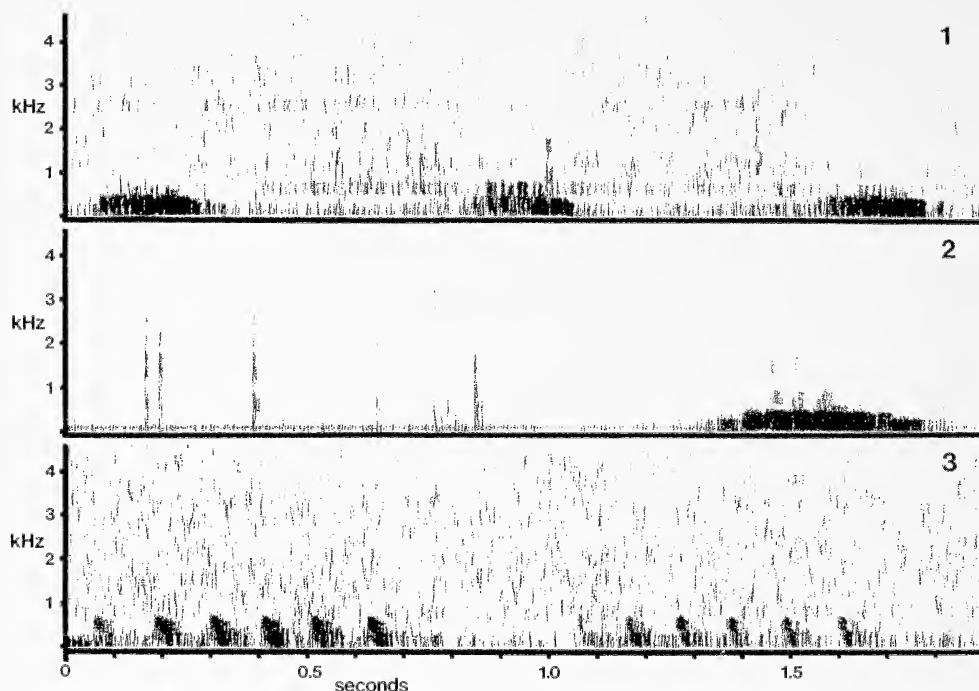
Matériel examiné.—EQUATEUR: LOS RIOS: Rio Palenque, 50 Km de Quevedo, 1 mâle, 1 femelle (RA), R. Alsina coll. CCRP, 1 janvier 1981, 2 mâles, 1 femelle (JB), S. Sandoval coll. Mars 1981, 1 femelle (JB), S. Sandoval coll. 26 décembre 1980, 1 mâle, 1 femelle (JB), S. Sandoval coll. PECHINCHA: Rio Peripá, 1895-98, 1 femelle-holotype (MIZSUT-Sc-5-274), L. Festa coll. 4 Km Sto. Domingo, 8 juin 1976, 1 mâle (FMNH), S. Peck coll. (Ber.-342, termite nest), 16 Km SE Sto. Domingo, 15 juin 1975, 1 femelle (FMNH), S. Peck coll. (Ber.-300, leaf litter), 47 Km S Sto. Domingo, Rio Palenque, 18 mai 1975, 2 mâles, 3 femelles (FMNH), S. Peck coll. (Ber. B-299A, forest litter), 25 février 1976, 1 femelle (FMNH), S. Peck coll. (Ber., decaying fruit).

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A COMMON METHOD OF SOUND PRODUCTION BY COURTING JUMPING SPIDERS (ARANEAE, SALTICIDAE)

There have been only a few reports of sound production by salticids (Bristowe 1929; Edwards 1981; Maddison 1982; Gwynne and Dadour 1985), spiders which have been thought to rely heavily on visual communication (Jackson 1982:246). Our recent recordings of jumping spider courtship have now confirmed that the behavior of abdomen twitching, widespread in the family, produces a sound, as anticipated by Jackson (1978, 1982:218), which is easily recorded and possibly significant. To record both sound and behavior, spiders were placed on a piece of light cardboard taped over a Pressure Zone Microphone® ("Sound Grabber", Crown, Inc.) connected to a Pentax™ Video Recorder which also received video input from a JVC™ color video camera (Model 6X-N74™ with 105 mm macro lens). Eighteen North American species were recorded: six *Habronattus* species (see Maddison and Stratton 1988), *Maevia inclemens* (Walckenaer), the dendryphantines *Eris aurantia* (Lucas), *Eris limbata* (Banks), *Metaphidippus watonus* Chamberlin & Ivie, *M. cf. manni* (Peckham & Peckham), *M. cf. galathea* (Walckenaer), *Phidippus cf. comatus* Peckham & Peckham, *Sassacus papenhoei* Peckham & Peckham, *Tutelina elegans* (Hentz), and *T. formicaria* (Emerton), and the euophryines *Habrocestum pulex* (Hentz) and *Tylogonus*



Figs. 1-3.—Sonograms of sounds made by abdominal twitching during dendryphantine courtship: 1, *Metaphidippus cf. manni*, showing sounds from three abdominal twitches; 2, *Phidippus cf. comatus* (the vertical streaks at left result from the palp hitting the substrate; the dark spot at right results from abdomen twitching); 3, *Sassacus papenhoei*, showing sounds from 11 abdominal twitches. Analyzed using a Kay Sonagraph 6061B®.

morosus (Peckham & Peckham). These species are all found frequently on foliage or leaf litter. In nine of these species, *E. aurantia*, *M. watonus*, *M. cf. manni*, *P. cf. comatus*, *S. papenhoei*, *Habronattus cognatus*, *H. conjunctus*, *H. elegans*, *H. borealis*, the males would occasionally twitch the abdomen down and up during courtship, at the same time emitting a buzzing or purring sound at frequencies mostly below 500 Hz (Figures 1-3; suitable sonograms were not obtained for *M. watonus* and *E. aurantia*). Though one would have expected the abdominal twitches to generate some vibrations, it was surprising that they were strong enough to be recorded as airborne sounds by our relatively crude equipment. The other species were not seen to twitch the abdomen nor were they heard to make such noises, except one subadult female of *Eris limbata* who buzzed her abdomen while a male was courting. In all species the abdomen contacts neither the substrate nor the carapace while twitching. The sound may be produced by the legs recoiling and striking the substratum on each of the abdominal twitches, although in most species these twitches appear gentle. Because this abdominal twitching is hidden and seems unlikely to function as a visual stimulus to the female (Jackson 1982), if it has a communicatory function at all it is probably via the vibrations produced and transmitted through the substrate, though this has yet to be tested experimentally. Given the ubiquity of abdominal twitching in salticid courtship, it therefore appears that acoustic communication in salticids may be the rule, rather than the exception.

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A FAUNAL SURVEY OF SPIDERS ASSOCIATED WITH *PINUS RADIATA* IN A SOUTHERN CALIFORNIA FARM

Spiders form an important predatory guild associated with coniferous trees. Their role as predators of lepidopterous pests in such ecosystems has been investigated by several researchers. Eickenbary and Fox (1968) reported spiders as the most abundant predators of the Nantucket pine tip moth (NPTM), *Rhyacionia frustrana* (Comstock), in loblolly pines, *Pinus taeda* L., in South Carolina. They also reported that adult NPTM were captured in webs of *Frontinella communis* (Hentz) and *Argiope aurantia* (Lucas); whereas both NPTM adults and larvae were preyed upon by *Metaphidippus galathea* (Walckenaer), *Misumenops asperatus* (Hentz), and *Peucetia viridans* (Hentz). Bosworth et al. (1970) studied the spiders associated with loblolly pines in Oklahoma. They found NPTM adults trapped in webs of *Cyclosa conica* (Pallas), *Mangora gibberosa* (Hentz), *Neoscona* spp. and *Frontinella pyramitella* (Walckenaer). Juillet (1961) considered spiders the most effective predators of the

European pine shoot moth, *Rhyacionia buoliana* (Schiff), due to their abundance and the different stages they attacked. Ohmart and Voigt (1981) sampled arthropods in natural and planted Monterey pine stands in California. Based on foliage samples, they reported spiders to comprise 33 percent of the total individuals and the most abundant arthropod group.

In California, NPTM is the key insect pest of Monterey pine, *Pinus radiata* D. Don, grown commercially as Christmas trees. Under southern California conditions, NPTM goes through four generations per season. This complicates management efforts and leads to poor control due to improper timing and misapplications of pesticides. Attempts by Scriven and Luck (1978; 1981) have been made to introduce parasites against this pest. This approach was successful in relatively undisturbed landscape settings. However, reliance on parasites for NPTM control in commercial Christmas tree production may not be feasible. This is due to frequent cultural practices and control measures directed toward other pests which may disrupt the host/parasite balance. Spiders, therefore, emerge as potentially valuable biological control agents in such high disturbance settings. Their merits lie in their high mobility, broad carnivorous feeding habits, and relatively high reproductive capability. The study reported herein was conducted to determine the relative seasonal abundance and species diversity of spiders in a commercial Christmas tree farm in southern California.

The study was conducted in 1986 on a 3-year-old stand of Christmas trees in Grand Terrace, San Bernardino County, California. Average tree height was 83 cm. Ground-associated spiders were monitored with pitfall traps similar to the method of Greenslade (1964). Eighteen traps were placed in the ground, spaced approximately 3.66 m (12 ft) apart. Traps were changed once every three weeks between April 24 and October 23. Samples were taken to the laboratory for determination and quantification. Foliage-associated spiders were sampled from 48 trees, utilizing the beat pan method modified from Bosworth et al. (1971). Sampling was conducted on May 30, July 9, September 19, and October 24. Kaston (1978) was used for familial, generic and, when possible, specific determinations. Calculations were made of richness (total number of families) and abundance (total number of individuals). Additionally, calculations were made on familial diversity through modification of the Shannon-Wiener index of species diversity: $H' = -\sum(n/N)\log(n/N)$; where " n " equals the number of individuals of a family in the sample and " N " equals the total number of individuals of all families in the sample.

Seventeen families, represented by 24 genera, were captured during the study (Table 1). Quantitative measurements of ground- and foliage-associated spiders are shown in Table 2. A larger number of families and a greater abundance of ground-associated spiders were noticed early in the season. As the season progressed, fewer numbers of a lesser amount of families were captured. This trend was reflected by diversity which was highest early in the season, but decreased by approximately 50 percent at the end of the study. The decrease in diversity was likely due to the family Lycosidae which was abundant throughout the season, but dominated in numbers during the latter part. The most commonly encountered genus in that family was the thin-legged wolf spiders, *Pardosa*.

Foliage-associated spiders also were abundant early but declined later in the season. Their diversity also was high at the early part of the study, decreasing by approximately 50 percent as the season progressed. Salticidae was the most

Table 1.—Spiders captured in a southern California Christmas tree farm, 1986.

| FAMILY | SCIENTIFIC NAME OF TAXA |
|----------------|--|
| Agelenidae | <i>Agelenopsis aperta</i> (Gertsch) |
| Amaurobiidae | (undetermined) |
| Anyphaenidae | <i>Aysha</i> sp. |
| Clubionidae | <i>Castianeria</i> sp.; <i>Trachelas deceptus</i> (Banks); <i>Trachelas</i> sp. |
| Dysderidae | <i>Dysdera crocata</i> C. L. Koch |
| Gnaphosidae | <i>Cessonia classica</i> Chamberlin; <i>Drassyllus</i> sp.; <i>Sergiolus</i> sp.; <i>Zelotes</i> sp. |
| Linyphiidae | (undetermined) |
| Lycosidae | <i>Alopecosa</i> sp.; <i>Lycosa</i> sp.; <i>Pardosa</i> sp. |
| Oecobiidae | <i>Oecobius annulipes</i> Lucas |
| Oxyopidae | <i>Oxyopes salticus</i> Hentz; <i>O. scalaris</i> Hentz |
| Philodromidae | <i>Ebo</i> sp. |
| Pholcidae | <i>Pholcus phalangioides</i> (Fuesslin); <i>Physocyclus californicus</i> Chamberlin & Gertsch |
| Pisauridae | (undetermined) |
| Salticidae | <i>Habronattus</i> sp.; <i>Phidippus johnsoni</i> G. & E. Peckham |
| Tetragnathidae | <i>Tetragnatha laboriosa</i> Hentz |
| Theridiidae | <i>Latrodectus hesperus</i> Chamberlin & Ivie |
| Thomisidae | <i>Misumena vatia</i> (Clerck); <i>Tibellus</i> sp.; <i>Xysticus</i> sp. |

frequently encountered family on the foliage throughout the season. The terms "ground-" and "foliage-associated," as used in this context, denote the methods by which spiders were captured. They do not necessarily imply specific habitat associations. The latter can be qualified by the facts that salticids were often captured in pitfall traps, and lycosids—especially *Pardosa*—were occasionally encountered on the foliage.

The spider fauna studied in this Christmas tree farm was most abundant and diverse early in the season. Early NPTM generations are considered more damaging than later ones, due to their feeding on young growing tips. It is conceivable that an abundant and diverse spider fauna during that period may result in a significant reduction in NPTM population through predation on several of the life stages consistent with observations by Juillet (1961). This

Table 2.—Quantitative measurements of ground- and foliage-associated spiders based on pitfall trap counts and beat pan samples, respectively, in a commercial Christmas tree farm, Grand Terrace, California, 1986.

| DATE | RICHNESS | ABUNDANCE | DIVERSITY |
|--------------------|----------|-----------|-----------|
| GROUND-ASSOCIATED | | | |
| May 8 | 10 | 79 | 0.7493 |
| May 30 | 11 | 111 | 0.6533 |
| June 20 | 9 | 143 | 0.4834 |
| July 11 | 7 | 87 | 0.5132 |
| Aug. 1 | 6 | 33 | 0.5733 |
| Aug. 22 | 7 | 63 | 0.3582 |
| Sept. 12 | 4 | 38 | 0.4169 |
| Oct. 3 | 6 | 58 | 0.3193 |
| Oct. 23 | 5 | 46 | 0.3823 |
| FOLIAGE-ASSOCIATED | | | |
| May 30 | 6 | 22 | 0.6921 |
| July 9 | 2 | 7 | 0.2342 |
| Sept. 12 | 3 | 4 | 0.4522 |
| Oct. 24 | 3 | 4 | 0.3469 |

percentage of biological control may then be supplemented with selective insecticides (insect growth regulators) to attain the desired degree of suppression. Therefore, careful manipulation of several components is needed to enhance the beneficial spider fauna in the highly-disturbed commercial Christmas tree agroecosystems.

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PREY HANDLING AND FOOD EXTRACTION BY THE TRIANGLE-WEB SPIDER *HYPTIOTES CAVATUS* (ULOBORIDAE)

Triangle-web spiders, *Hyptiotes cavatus* (Hentz), emerge from egg sacs as second instars, begin constructing prey-capture webs when they enter the third stadium, and mature as sixth instars (Opell 1982). During an earlier laboratory rearing study of developmental rates and web production (Opell 1982), I also collected prey remains and recorded prey handling times. Here, I describe the prey necessary for the maturation of *H. cavatus*, trace developmental changes in its prey handling times and prey extraction rates, and evaluate the feeding efficiencies of each of its instars.

Table 1.—Prey consumption and prey extraction during *Hyptiotes cavatus* development.

| INSTAR | PREY CONSUMPTION | | | PREY EXTRACTION (mg dry weight) | | |
|--------|------------------|----------------------|-----|------------------------------------|-------------------------|---------------|
| | No. Spiders | Mean No. Prey/Spider | SD | No. Prey | Mean Extraction Per Fly | Stadium Total |
| 3rd | 21 | 3.9 | 1.8 | 72 | 0.08 | 0.32 |
| 4th | 21 | 2.8 | 0.7 | 59 | 0.16 | 0.43 |
| 5th | 21 | 4.7 | 1.3 | 97 | 0.15 | 0.64 |
| 6th | — | — | — | 86 | 0.16 | — |
| Total | 14 | 11.0 | 2.6 | | | |

All spiders used in this laboratory study were reared from egg sacs and were individually housed in plastic containers that measured $30 \times 16 \times 8.5$ cm. Wooden dowel rods cemented into each container provided web attachment sites. Spiders were kept at 23-25°C and 85-95% relative humidity and maintained on a 10:14 hour light:dark cycle. I checked these spiders daily and blew one wild type *Drosophila melanogaster* (both males and females were used) into each web they produced. I recorded the duration of a complete prey wrapping sequence and from this subtracted periods of inactivity and prey transport to obtain actual prey wrapping time. I began timing feeding when a prey's thick silk swathing became transparent as it absorbed digestive enzymes, checked specimens every 10-15 minutes thereafter, and noted when the spider had discarded its prey.

These extracted prey were collected, placed in a vacuum desiccator with desiccant, and stored until the study was completed four and one-half months later, at which time they were pooled by instar and weighed on a Metler® H-31 AR balance. At 6-8 week intervals during this study, three samples of 100 fruit flies each were taken from the stock cultures used to feed the spiders, placed in a clean vial, heat-killed by holding the vial over a steam jet for 5 seconds, spread on filter paper, and placed in a vacuum desiccator. From the mean dry weight of these flies (0.19 mg, range 0.17-0.23 mg), I subtracted the mean dry weight of the prey discarded by spiders of each stadium to obtain prey extraction values.

Table 1 summarizes the number of prey consumed during each stadium and the amount of material extracted from each prey. The numbers of prey eaten by males and females are combined because *t*-tests reveal no significant difference ($p > 0.05$) between them. Only the mean numbers of flies eaten by fourth and fifth instars differ significantly ($p < 0.05$) when compared with *t*-tests.

The amount of material spiders extract from flies doubles after the third instar, but shows no increase thereafter (Table 1). The small size of third instars may limit the volume of digestive enzymes they can produce and make available to them only half the potential food of a fruit fly. Although the number of prey consumed by third and fourth instars does not differ significantly, this increased extraction by fourth instars is responsible for their having a 34% greater total prey extraction (mean number of prey consumes \times mean extraction) than third instars. The greater number of flies eaten during the fifth stadium results in a further 49% increase in food intake.

Table 2 documents a 77% decrease in wrapping time and an 84% decrease in feeding time from third to sixth stadia. The percentage of prey handling time devoted to wrapping drops by half after the third stadium, but remains constant thereafter. Extraction efficiency increases during development, with fourth instars

Table 2.—Developmental changes in *Hyptiotes cavatus* prey handling. All times are in hours. Extraction values are in mg dry weight.

| INSTAR | WRAPPING TIME | | | FEEDING TIME | | | TOTAL TIME PER FLY | | | | mg EXTRACTED PER HOUR FEEDING |
|--------|---------------|------|------|--------------|-------|------|--------------------|-------|------|---------------|--|
| | No. | Mean | SD | No. | Mean | SD | No. | Mean | SD | % Wrapping | |
| 3rd | 31 | 0.44 | 0.22 | 21 | 6.55 | 4.31 | 11 | 6.25 | 4.54 | 7 | 0.012 |
| 4th | 35 | 0.34 | 0.12 | 10 | 10.31 | 4.18 | 10 | 10.67 | 4.25 | 3 | 0.016 |
| 5th | 42 | 0.22 | 0.06 | 20 | 5.21 | 1.42 | 20 | 5.41 | 1.42 | 4 | 0.029 |
| 6th | 20 | 0.13 | 0.05 | 12 | 3.06 | 0.70 | 12 | 3.18 | 0.73 | 4 | 0.052 |

acquiring 1.3 times more food per hour of feeding than third instars and fifth and sixth instars each removing 1.8 times more food per hour than subsequent instars (Table 2).

The laborious prey wrapping characteristic of uloborids (see Lubin 1986 for a review) may compensate for their lack of poison glands and their inability to inject prey. Lubin (1986) found that prey type and mass influence the thoroughness of uloborid wrapping. All spiders of this study were fed the same type of prey and, judging by the opacity and smoothness of the wrapped flies, wrapping thoroughness remains relatively unchanged during development. Therefore, the shorter wrapping times characteristic of later instars probably reflect increases in the aciniform silk glands and spigots used in prey wrapping (Foelix 1982) and reductions in the time required for spiders to circumscribe a prey during early wrapping stages and to manipulate a partially swathed fly during latter wrapping stages.

Together with the previous developmental study of *H. cavatus* (Opell 1982), these results emphasize the small cost of web production. Accidental web damage caused spiders to receive an average of only 0.84 flies per web constructed. Despite this, their development times did not differ markedly from those of natural populations.

Although wrapping and feeding times differ among instars, the proportion of each stadium's "web construction" phase (Opell 1982) devoted to prey handling remains surprisingly small and constant. Third instars devote 4.8% of this time to prey handling, fourth instars 7.3%, and fifth instars 5.5%.

Matthew H. Greenstone and Yael D. Lubin made useful comments on this manuscript.

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SPIDER PREDATORS OF MOSQUITO LARVAE

Spiders have been largely overlooked as predators of mosquito larvae in aquatic ecosystems. Bishop and Hart (1931) were the first to report a spider (*Pardosa sternalis* (Thorell)) consuming mosquito larvae in a small gravel pit pool in Colorado. Garcia and Schlinger (1972) also reported consumption of mosquito larvae by *P. sternalis*. The mosquitos involved in the latter instance were *Aedes dorsalis* (Meigen) breeding in a California salt marsh. Similarly, Greenstone (1979, 1983) reported evidence of predation of *Ae. dorsalis* by *Pardosa ramulosa* (McCook). *Dolomedes* sp. was found to prey upon ^{32}P -labeled *Culex pipiens pipiens* L. larvae in a Southeast Texas ricefield (Breene, unpubl. data). Finally, Service (1973) found a species of *Lycosa* and one of *Pardosa* testing positive for *Anopheles gambiae* Giles in a precipitin analysis, but implied they probably attacked only emerging mosquito adults.

In the current study, a pisaurid, *Dolomedes triton* (Walckenaer), and two lycosids, *Pirata sedentarius* Montgomery and *Pardosa delicatula* Gertsch & Wallace, were evaluated as predators of *C. p. pipiens*, the northern house mosquito. *Dolomedes triton* and *P. sedentarius* were chosen for their close association with mosquito larvae habitats in East Texas, while *P. delicatula* was chosen due to its common presence in grassy areas that border much of the mosquito larvae habitat in the College Station, Texas area. The results of these evaluations are reported within.

METHODS

Fourth instar *C. p. pipiens* larvae from laboratory cultures were irradiated with 0.1 to 0.4 $\mu\text{Ci/ml}$ ^{32}P for 24 h in a 500 ml container, and then were removed and washed thoroughly to remove residual radioactivity from the integument. A mean DPM (disintegrations per minute) for the mosquito larvae ($n=50$) was determined from a random sample of larvae before each experiment.

Approximately 1000 radioactive larvae were placed into each of two simulated grass bank ponds, each measuring 110 cm by 70 cm and filled with water to a depth of 8 cm. These ponds were set up in aquarium tanks lined with black plastic tarp to facilitate rapid removal of any radioactive residues between experiments. Approximately 25% of the surface of the water in each pond was covered with duckweed (*Wolffia papulifera* Thomps. and *Spirodela ologorhiza* (Kurtz) Hegelm) and grass debris (*Cynodon dactylon* (L.)) to simulate natural pond conditions. An additional 1000 non-radioactive mosquito larvae were placed in an identical control tank.

The first simulated pond contained only spiders captured on or near local ponds. The second pond contained both spiders and several of the 30 species of aquatic insect predators also found in local ponds that were used over the course of the experiments. In the case of the control, 1000 non-radiated mosquito larvae were placed in a simulated pond containing both spiders and insects. Otherwise, the control pond was similar in all aspects to the test ponds. After 48 h, all spiders and insects were removed from the test and control ponds and subjected

individually to liquid scintillation counting procedures. Seventeen replications were performed.

A simple linear algorithm was used to estimate quantitative ingestion of larvae by the three species of spiders. Observation of predation of a known number of mosquito larvae with a known radioactive mean by each species of spider was used to derive the quantifying algorithm. A complete and detailed account of ^{32}P quantitative methods can be found in Breene & Sterling (1988).

RESULTS AND DISCUSSION

A total of 56 of 73 (76.7%) *D. triton* exposed to ^{32}P - labeled mosquito larvae were found labeled with ^{32}P . An average of 12 mosquito larvae per 24 h were consumed by these labeled spiders. Only six *D. triton* used in the study were adult, of which half were radioactive, indicating larval consumption.

In the case of *P. sedentarius*, 118 of 160 (73.8%) of the spiders consumed an average of two mosquito larvae per 24 h. However, only 17 of 56 (30.4%) *P. delicatula* tested positive for radioactivity. Of the *Pirata* and *Pardosa* utilized, 106 of 160, and 51 of 56 were adults, respectively.

No significant differences were found in predation rates between any of the spider species in either the tank with spiders only or in the tank where the spiders were given a wider choice of prey in the form of other insects. Both *Dolomedes* and *Pirata* were observed preying upon the mosquito larvae by grasping individual larvae from beneath the surface of the water, pulling their bodies through the surface tension and consuming them.

Dolomedes triton and *P. sedentarius* share habitat preferences in common with mosquito larvae (Carico 1973; Wallace and Exline 1978; Heiss and Meisch 1985). In Texas, these spiders most notably associate with riceland populations of *Psorophora columbiae* (Dyar and Knab) and a salt marsh mosquito, *Aedes sollicitans* (Walker). *Pardosa delicatula* is often found along the banks of ponds and streams but has not been closely tied with the aquatic habitat. However, other species of *Pardosa* have been found in such habitats (Bishop and Hart 1931; Garcia and Schlinger 1972; Greenstone 1979, 1980; Heiss and Meisch 1985). *Dolomedes triton* and many species of *Pirata* are found commonly associated with mosquito larva habitats except during reproductive or migrational cycles. In salt marshes, hunting spiders such as *Pirata* (LaSalle and Cruz 1985) and *Dolomedes* (pers. obs.) may be highly important invertebrate predators of mosquito larvae due to the paucity of freshwater aquatic insect predators known to prey upon mosquito larvae.

This study furnishes laboratory evidence that the three species of spiders tested will prey readily upon mosquito larvae. If a complete picture of the predation ecology of culicine larvae is to be ascertained, field work that includes entire groups of potentially important taxa, such as the Araneae, will be required.

Sincere appreciation is extended to C. D. Dondale for identification of the lycosids and to C. Burandt for identification of the botanical specimens. Many thanks go to D. A. Dean, P. M. Langan, J. Langan and S. Stewart for helpful suggestions involving the manuscript. Portions of this study were supported in part by grants from the U.S. Environmental Protection Agency and the USDA Special Grants Office (Grant No. CR806771-03).

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REGINALD FREDERICK LAWRENCE, 1897-1987

Dr. Reginald Frederick Lawrence, dean of African Arachnology, died in Pietermaritzburg, South Africa on October 9, 1987 at the age of 90, after a brief illness. He left behind a legacy of contributions to science in general and Arachnology in particular which spanned more than 60 years.

Dr. Lawrence was born in the small coastal town of George in the Cape Province of South Africa on March 6, 1897. He was educated from 1908 to 1913 at Saint Andrew's College in Grahamstown, and he matriculated from Tulbagh High School in 1915. He went on to study at the University of Cape Town (then the South African College), but his studies were interrupted by World War I. He spent two years as an infantryman in France, being wounded in 1918. After recovering from his wounds, he returned to his University studies and graduated with his B.Sc. in 1922.

In 1922 he joined the Staff of the South African Museum in Cape Town. At that time his knowledge of Arachnids was minimal, and the then director of the Museum, Dr. Peringuey, hurled the two huge volumes of Simon's *Histoire Naturelle des Araignées* at him and ordered him to absorb the contents if he wanted a job. Borrowing a French dictionary, he succeeded in this task and was appointed on probationary status as assistant in charge of Arachnida, Myriopoda, Reptilia, and Amphibia. The appointment was subsequently made permanent, and he remained at the South African Museum until 1935. During his early years at the South African Museum he began the extensive course of fieldwork that was to mark his entire career. His first collecting expedition in 1923 was to Moçambique, where he traveled alone, much of the time by donkey-back, along the undeveloped coast. For three months each during 1923/1924/1925 he journeyed north into South West Africa, first by rail to the northern part of the territory, and then via ox or donkey wagon through Ovamboland, the Kaokoveld, and to the Angolan border. Lawrence was the only expedition member who could shoot, and his fellow expedition members depended on him to fill the pot with fresh meat, usually springbok, which were then present in many thousands. The extensive collection of Arachnida made during these trips formed the basis for his doctoral thesis, for which he received his Ph.D. from the University of Cape Town in 1928.

In 1935 Dr. Lawrence was appointed Director of the Natal Museum in Pietermaritzburg, where he remained until his retirement in 1964. He edited the *Annals of the Natal Museum* from 1935 until 1964. It was during his time at the Natal Museum that he developed his keen interest in the cryptic fauna of the indigenous forests of southern Africa, culminating in his masterpiece of synthesis, *The Biology of the Cryptic Fauna of Forests*, published in 1953. He recognized the ancient distributional patterns shown by many of these small animals, and appreciated parallel relationships of the African forest biota to other tropical areas and to other temperate southern continents. His pioneering work on southern African forest biogeography serves as an inspiration for a new generation of arachnid biogeographers.

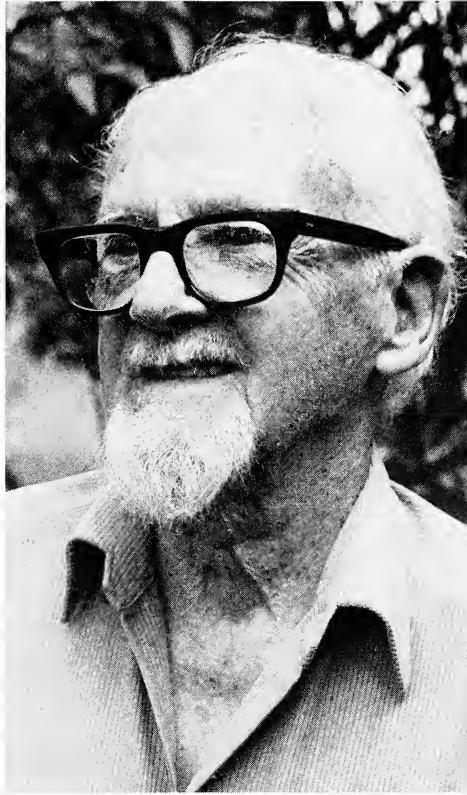


Fig. 1.—Dr. R. F. Lawrence in 1984 in Pietermaritzburg, South Africa, on the occasion of this 87th birthday. (Photo by P. M. C. Croeser)

Dr. Lawrence was a superb collector, and much of the new material described by him was from his own collections. During his tenure at the Natal Museum he visited indigenous forests from the southern Cape to the Limpopo River, and from the Indian Ocean coast to the crest of the Drakensberg Mountains. During these excursions he was accompanied and assisted by his wife, Ella Thompson Pratt Yule. In addition, he visited and made collections in Madagascar, Mauritius, Moçambique, South West Africa, and Zimbabwe (then southern Rhodesia). The collections amassed by him continue to be a treasure trove of new and exciting taxa, particularly those showing Gondwanan affinities.

Dr. Lawrence published 210 scholarly papers and books during a period spanning nearly 60 years. These covered a wide range of topics, including natural history, biogeography, museology, and the taxonomy and biology of Acarina, Araneae, Chilopoda, Diplopoda, Onychophora, Opiliones, Pedipalpi, Pseudoscorpiones, Reptilia, Scorpiones, Solifugae, and Uropygi. His last book, *The Centipedes and Millipedes of Southern Africa: a Guide*, was published in 1984.

He received numerous honors during his career. In 1935 he was elected a fellow of the Royal Society of South Africa; he was elected President of the Entomological Society of Southern Africa in 1953; in 1956 he was awarded the Medal and Grant of the South African Association for the Advancement of Science, and in 1958 was elected President of Section D of that same society; in 1964 the Natal Museum published a Festschrift in his honor; in 1973 he was

awarded the Medal of the Zoological Society of South Africa; in 1985 he was made an honorary member of the American Arachnological Society; and in 1986 he was made an honorary life member of the South African Museums Association. More detailed biographical sketches may be found in the *Annals of the Natal Museum*, vol. 16, pp. i-ix, 1964; and *American Arachnology*, vol. 21, pp. 13-15, 1980.

Throughout his scientific career, through his retirement, and up until the end of his life, Dr. Lawrence remained a true humanitarian. He was generous, courteous, humble and kind, qualities which he showed to friends and colleagues at all times. Throughout his life he was a solicitous and dedicated correspondent, and spared no effort to be of assistance to established scientists and students alike. Not a letter was received, even from persons that he had never met, that did not receive a careful response. I remember him, at the age of 88, mounting a search in the rugged montane forests of Natal for live specimens of Onychophora which were essential to the doctoral research of a student in Europe. The walking worms were captured alive and duly dispatched via the post to Germany. He was frequently acknowledged for his advice to and efforts on behalf of interested naturalists from around the world. He was a source of support and inspiration to Arachnologists throughout Africa and beyond.

Dr. Lawrence leaves behind two sons, Alastair and Jonathan, two sisters, and many friends and colleagues whose privilege and good fortune it was to have known "Lawrie" during his long and productive life.

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The American Arachnological Society was founded in August, 1972, to promote the study of Arachnida, to achieve closer cooperation between amateur and professional arachnologists, and to publish *The Journal of Arachnology*.

Membership in the Society is open to all persons interested in the Arachnida. Annual dues are \$30.00 for regular members, \$20.00 for student members and \$50.00 for institutions. Correspondence concerning membership in the Society must be addressed to the Membership Secretary. Members of the Society receive a subscription to *The Journal of Arachnology*. In addition, members receive the bi-annual newsletter of the Society, *American Arachnology*.

American Arachnology, edited by the Secretary, contains arachnological news and comments, requests for specimens and hard-to-find literature, information about arachnology courses and professional meetings, abstracts of papers presented at the Society's meetings, address changes and new listings of subscribers, and many other items intended to keep arachnologists informed about recent events and developments in arachnology. Contributions for *American Arachnology* must be sent directly to the Secretary of the Society.

†Deceased

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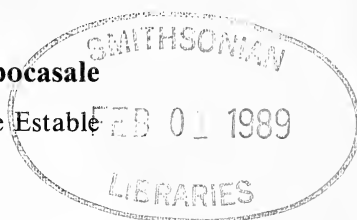
REVISION OF THE GENUS *PYCNOTHELE* (ARANEAE, NEMESIIDAE)

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ABSTRACT

On the basis of a character analysis, the genus *Pycnothele* and species attributed to *Androthelopsis* were revised and it was concluded that *Pycnothele* Chamberlin, 1917 = *Androthelopsis* Mello-Leitão, 1934. The genus *Pycnothele* comprises three species that are redescribed and illustrated: *Pycnothele auronitens* (Keyserling, 1891) (= *Androthelopsis modestus*: Raven, 1985 (in part.) and *Psalistops auripilus* Mello-Leitão, 1946 new synonyms); *Pycnothele perdita* Chamberlin, 1917; and *Pycnothele singularis* (Mello-Leitão, 1934) new combination (= *Pycnothelopsis modestus* Schiapelli & Gerschman, 1942 and *Androthelopsis modestus*: Raven, 1985 (in part) new synonyms). *Heteromma anomala* Mello-Leitão, 1934, although it belongs to *Pycnothele*, is an uncertain species. A taxonomic key is included for species identification.

INTRODUCTION

Pycnothele was created by Chamberlin (1917) based on the type of *Pycnothele perdita*, from Brazil. This genus includes medium-sized species (usually 20 to 30 mm in body length) found only in South America (Argentina, Brazil and Uruguay).

Schiapelli & Gerschman (1942) created the genus *Pycnothelopsis* and placed it together with *Pycnothele* in the family Pycnothelidae. These taxa were revised by Mello-Leitão (1934, 1946), Schiapelli & Gerschman (1942), Schiapelli & G. de Pikelin (1965, 1967, 1971), Gerschman de Pikelin & Schiapelli (1970), Capocasale & Pérez-Miles (1979), Pérez-Miles & Capocasale (1982, 1983) and Raven (1985). Recently Raven (1985) has analyzed the infraorder Mygalomorphae, clarifying the relationships of families. As a result of this analysis, *Pycnothele* and *Androthelopsis* were placed in the family Nemesiidae and *Pycnothelopsis* was designated as a junior synonym of *Androthelopsis*.

The repeated changes of place of the species of these genera and controversies among the authors reveal uncertainty about the correct placing of such taxa and their systematic relations. The diagnostic characters separating *Androthelopsis* and *Pycnothele*, apparently clear in the literature, appear to us to be inaccurate or conflicting. Doubtless, the low number of species in these genera has contributed to maintaining restrictive diagnostic criteria for them, a practice which we feel is unjustified. The small number of available specimens has also made the study of intraspecific variation difficult and prejudiced the specific diagnoses and identification.

As a result of the character analysis we have made on all material available in collections, (1) the species attributed to these genera are distinguished and characterized and (2) their systematic relations are clarified. The election of *Pycnothele* and *Androthelopsis* as a unit for study is based on the systematic proximity of these genera, which have traditionally been linked and are now considered sister groups (Raven 1985:45). A key conclusion of our present study is that *Pycnothele* = *Androthelopsis*.

METHODS

All drawings were made with a camera lucida and the measurements with an ocular micrometer; carapace measurements are accurate to 0.1 mm, eye and bulb measurements to 0.025 mm.

Computer programs were the Presta package developed in the Centro Ramón y Cajal, España. In the Student's *t*-test, the confidence limit was $P=0.05$; in the correlation calculation, the confidence limit was 95%. In the analysis of character polarity (group under study: species attributed to *Pycnothele* and *Androthelopsis*), *Neodiplothele* Mello-Leitão was used as out-group. The selection of the out-group was based on the results given by Raven (1985:45).

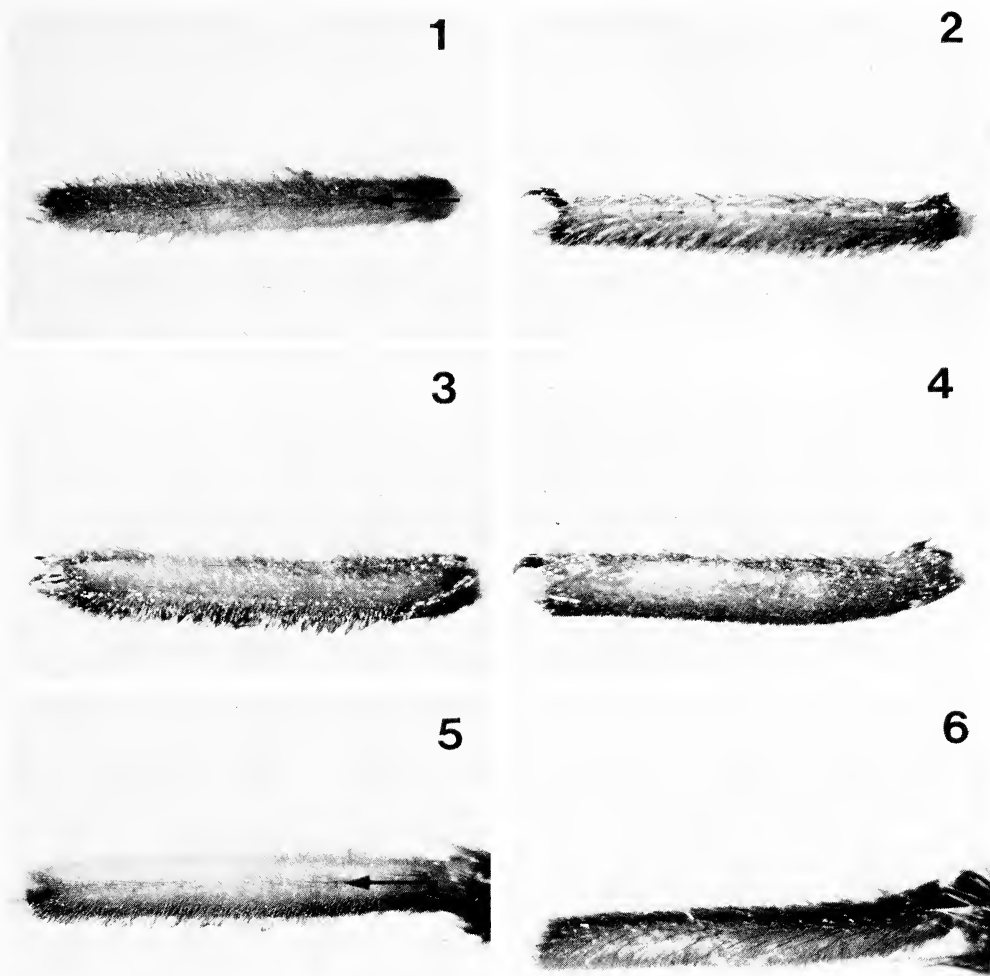
Abbreviations.—British Museum (Natural History), London, England (BMNH); Instituto Butantan, São Paulo, Brazil (IB); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentine (MACN); Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ); Museo Nacional de Historia Natural, Montevideo, Uruguay (MNHN). AME= anterior median eyes; ALE= anterior lateral eyes; PME= posterior median eyes; PLE= posterior lateral eyes.

CHARACTER ANALYSIS

Integral/pseudosegmented tarsi.—This character was introduced into the systematics of Pycnothelinae by Raven (1985:11). The criteria used to define the pseudosegmented character state were “. . . tarsi have either a ventral transverse suture (“cracked”), or the cuticle of the lower surface is pallid and has shattered appearance like drying mud (“pseudosegmented”). Pseudosegmented tarsi appear either bent or curved”. The definition of this character is considered undesirable because it implies, at least, three attributes reduced to a double state character. Each attribute could vary independently and no homologies can be established among them. We think it is correct to develop it into three characters: cracked / not cracked; curved / not curved; and pallid / not pallid.

Raven (1985:100) used only the integral tarsi of females to distinguish between *Pycnothele* and *Androthelopsis*. Such a character is not comparable because females of *Androthelopsis* are unknown.

Raven (1985:100 and 101) mentioned tarsi I-II (in males of *Pycnothele*) and (apparently) I-IV (in *Androthelopsis*) as being pseudosegmented. We examined the types and did not observe “cracked” tarsi in either *Pycnothele* or *Androthelopsis* (Figs. 5 and 6). Species attributed to both genera have tarsi lightly curved (Figs. 2, 4, 6). The pallid condition of the tarsi shows intraspecific



Figs. 1-6.—Tarsi IV from holotype males of species of *Pycnothele*: 1, 3, 5, ventral views; 2, 4, 6, lateral views; 1, 2, *P. auronitens* (= *P. auripilus* = *A. modestus* [in part]); 3, 4, *P. perditia*; 5, 6, *P. singularis* (= *A. singularis* = *A. modestus* [in part]). Arrows show the stripe of longer setae dividing scopulae (scopulae divided).

variation, which also would be an artifact of preservation. The absence of morphological gaps in these characters do not support the separation of genera.

Entire/divided scopulae on tarsi IV.—The character entire/divided scopulae, has been traditionally used in the systematics of Mygalomorphae to separate genera and subfamilies (Schiapelli & Gerschman 1973:43). The type of *P. perditia* presents entire scopulae on tarsi IV (Fig. 3). The holotype and other specimens of *P. auronitens* examined and species attributed to *Androthelopsis* by Raven (1985:101 and 102) present the scopulae on tarsi IV longitudinally divided by a stripe of longer setae (Figs. 1 and 5). Raven (1985:100) described scopulae on tarsi IV as entire in *Pycnothele* (males); our results confirm that description for *P. perditia*; however, the type of *P. auronitens* presents divided scopulae on tarsi IV. There are two ways to interpret this: (1) *P. auronitens* is either misplaced in *Pycnothele* or (2) the character lacks diagnostic value. *Neodiplothele* has divided

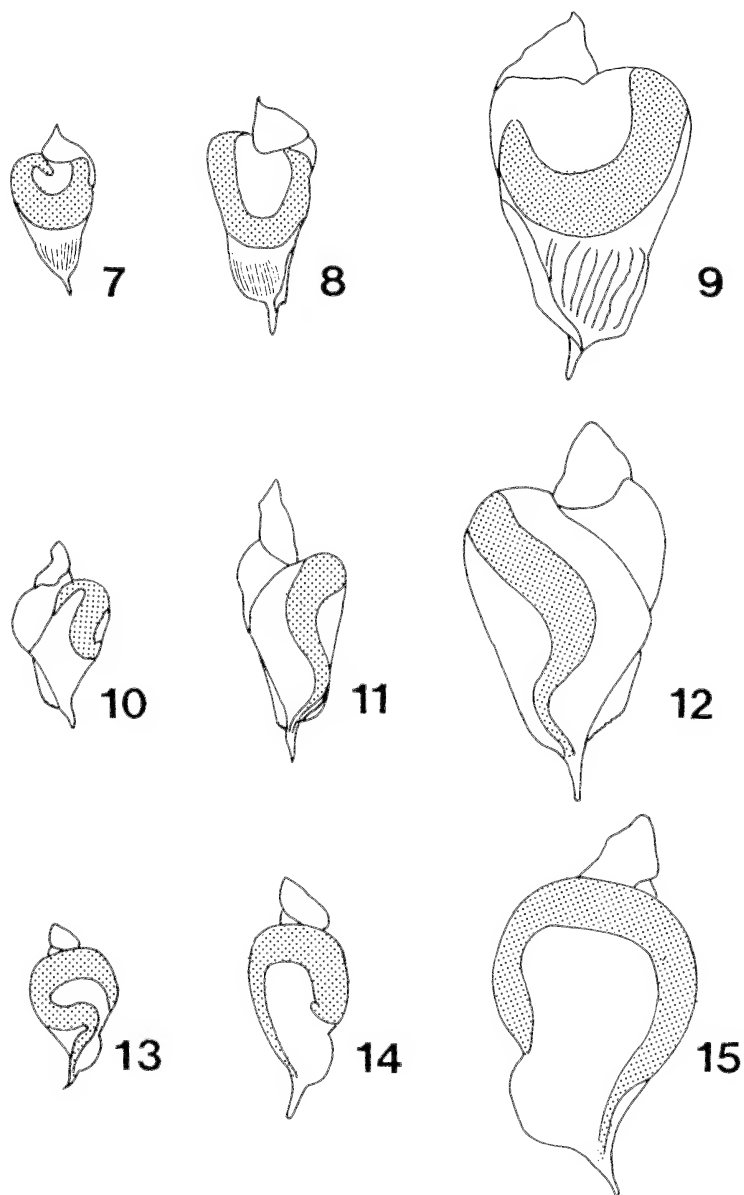
scopulae on tarsi IV (Raven 1985:102); by out-group comparison, divided scopulae constitute a plesiomorphy. By the criterion of ontogenetic precedence, scopulae division disappears during growth in some Mygalomorphae (Theraphosidae) (Schiapelli & Gerschman 1973:43); this would corroborate such hypothetical polarity. In the group under study, entire scopulae on tarsi IV can be interpreted as an autapomorphy of *P. perdit*. Therefore, this character appears to be diagnostically useless in these genera. It does not support the separation of genera.

Palpal bulb morphology.—The species attributed to *Pycnothele* and *Androthelopsis* present palpal bulbs with similar morphology. They are pyriform with a conspicuous subapical constriction and a short (5-9% of the bulb length) and narrow (5-10% of maximum bulb width) embolus. Bulbs possess subapical wide vanes, considered as a synapomorphy in these taxa (Raven 1985:45).

In *Pycnothele*, Raven (1985:100) describes: "very high vanes" and in *Androthelopsis* (1985:101): "high vanes". In the study of the types and other material examined, it was observed that vane height varies directly with bulb size ($r = 0.769$, $p < 0.01$), and body size ($r = 0.755$, $p < 0.05$). Bulb size was also correlated with body size ($r = 0.984$, $p < 0.01$). The difference pointed out for this character does not constitute a morphological discontinuity that permits a clear delimitation of states. Still, if one were to consider the "very high vanes" state as differentiable (ignoring the correlation with bulb size), it would be exclusively applicable to *P. perdit* (which has bulbs of perceptibly greater size than the remaining species studied). This condition could be interpreted as a specific autapomorphy, without importance in the separation of genera. Consequently, this character appears to be of no value in separating *Pycnothele* from *Androthelopsis*.

The species attributed to *Pycnothele* and *Androthelopsis* share the presence of a well differentiated embolus, short and narrow, that can be distinguished from the rest of the Pycnothelinae. In bulbs having a well differentiated embolus, the short embolus has been considered as plesiomorphic of the Nemesiidae (Raven 1985:80). In the Pycnothelinae, excepting the group submitted to study, the rest of the genera have bulbs with the embolus little or not differentiated (*Neodiplothele*, *Rachias*, *Pselligmus*); or differentiated and long (*Chaco*). According to Raven, (1985:45) *Neodiplothele* is a sister genus of *Pycnothele* plus *Androthelopsis*; *Chaco* is a sister genus of these three. These facts question the mentioned polarity for embolus characters. However, the data are too fragmentary to reach any conclusion. Omitting the polarity of such characters and analyzing them in terms of similarity, embolus morphology becomes useful to distinguish the species attributed to *Pycnothele* and *Androthelopsis* from the rest of the Pycnothelinae.

In the Mygalomorphae, the bulbal duct ("spermophor") is sclerotized in part of its length and it often appears fused with the exterior bulb wall (Kraus 1984:377). This secures the stability of such a structure for its use as a systematic character. The tract of the bulbal duct can be directly observed through the bulb cuticle in Pycnothelinae. *P. auronitens* (= *P. auripilus*) has the subterminal part of the duct strongly curved, in the proximal sense (Figs. 10, 13). This character differs perceptibly from that of other species studied (Figs. 11-15). It is not possible to determine the polarity of these bulbal duct character states due to absence of data in the out-group; however, they clearly distinguish *P. singularis* (= *P. modestus*)



Figs. 7-15.—Palpal bulbs from holotype males of species of *Pycnothele*: 7-9, dorsal views; 10-12, ventral views; 13-15, prolateral views; 7, 10, 13, *P. auronitens* (= *P. auripilus* = *A. modestus* [in part]) (left bulb); 8, 11, 14, *P. singularis* = *A. singularis* = *A. modestus* [in part]) (left bulb); 9, 12, 15, *P. perditia* (right bulb). Shaded area represents visible tract of bulbal duct.

and *P. auronitens* (= *P. auripilus*). Differences in bulb morphology between the types of *P. auronitens* and *P. auripilus* were not found. The bulb of the type of *P. auripilus* is more pallid, possibly due to the use of clearing techniques or to the preservation method. This fact probably made observation of the structures difficult for the previous authors. Except for a little difference in size, other differences in bulb morphology between the types of *A. singularis* and *A. modestus* were not found. Bulbal duct tract is considered useful as a specific character.

Cuspules.—The presence of cuspules on maxillae is shared by all species attributed to *Pycnothele* and *Androthelopsis*. Number of maxillary cuspules was used as a diagnostic character between *Pycnothele* and *Pycnothelopsis* (sub *Androthelopsis*) by Schiapelli & G. de Pikelin (1967). Capocasale & Pérez-Miles (1979) analyzed the value of this character in *Pycnothelopsis*, discarding it as generic and specific character because it overlaps with the mentioned values for *Pycnothele* and because it presents high intraspecific variability. These results were confirmed in the present analysis. Raven (1985:79) considers the presence of maxillary cuspules as a plesiomorphy of Nemesiidae; this criterion agrees with our results in the group submitted to study.

The presence of cuspules on the labium is shared by the species of the group under study (Figs. 16-18), except in the type of *Heteromma anomala*. This character was used by Schiapelli & G. de Pikelin (1967). Capocasale & Pérez-Miles (1979) concluded that like the maxillary cuspules, it lacks diagnostic value at the generic or specific level in *Pycnothelopsis* (sub *Androthelopsis*).

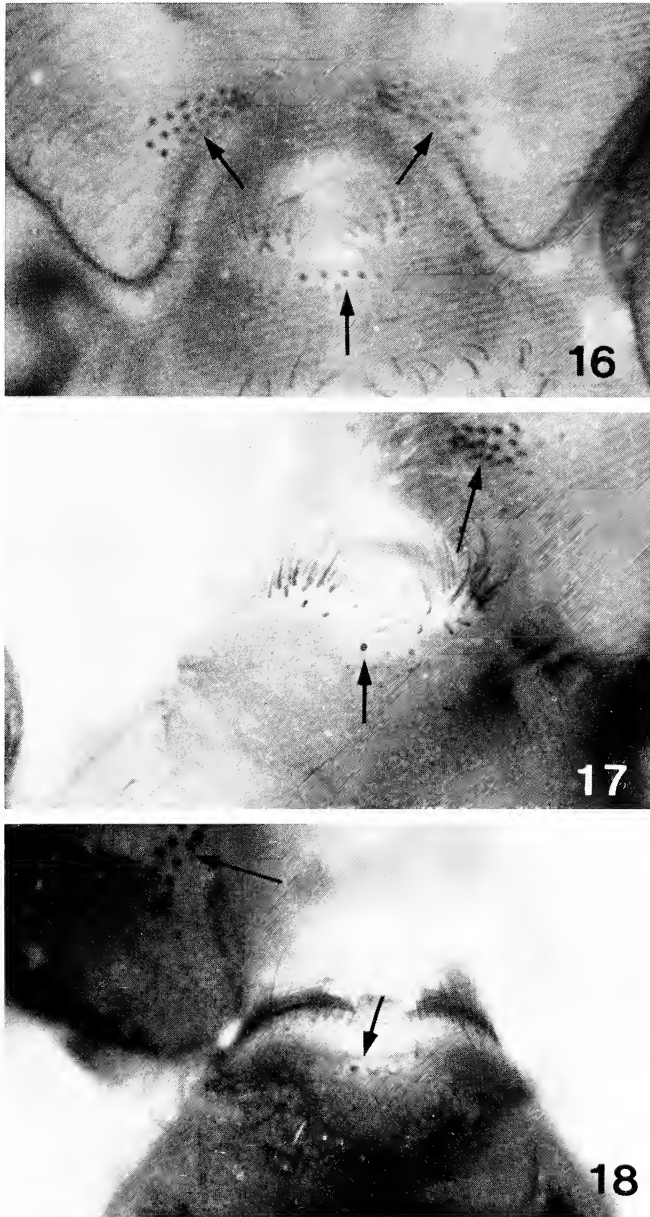
Raven (1985:100, 101) indicated "No cuspules on labium" in the descriptions of both genera. This statement is only valid for the type of *H. anomala* but does not have a factual basis for other species studied. It was not possible to establish the polarity of the labial cuspules in the Pycnothelinae. However, Raven (1985:79) indicated that "labium with few cuspules" would represent a plesiomorphy in Nemesiidae.

According to the results obtained, we conclude that both maxillary cuspules and labial cuspules do not support the separation of genera.

Eyes.—Eye dimensions have been used as diagnostic characters separating *Pycnothele* and *Pycnothelopsis* (sub *Androthelopsis*) by Schiapelli & G. de Pikelin (1967).

The correlation analysis between eye dimensions (maximum diameter) and body size (length of carapace) in the specimens of the group under study, gave the following results: AME/carapace $r=0.805$; ALE/carapace $r=0.932$; PME/carapace $r=0.737$; PLE/carapace $r=0.854$. These values indicate a significant correlation at the 95% level. This leads us to question the systematic value of this character, as it is empirically correlated with size.

To avoid variations due to size of specimens, eye dimensions were studied in a relative way (maximum diameter/carapace length). Significant differences in the relative dimensions of eyes between the type of *P. perditus* and the sample of *P. singularis* (= *A. singularis* = *P. modestus*) were not found. In the comparison of *P. perditus* with *P. auronitens* (= *P. auripilus* = *A. modestus* in part) AME and PME presented significant differences ($t=10.42$; $P<0.001$ and $t=4.02$; $P<0.02$ respectively). Significant differences for ALE and PLE were not found. (In the type of *P. auronitens* the right PLE is ectopic and of lesser size. It was not used in the comparison). In the comparison between the samples of *P. auronitens* and *P. singularis* only ALE show significant differences ($t=2.04$; $P<0.05$). The two species placed in different genera (*P. perditus* and *P. singularis*) by Raven (1985:100, 101) do not show differences in these characters. *P. perditus* and *P. auronitens* placed by Raven (1985:100) in the same genus, have differences in the relative size of AME and PME. Taking into account the absence of data that could permit us to determine polarity of these characters, and the results obtained, they are considered to be specific level characters. Such characters do not support the separation of genera.



Figs. 16-18.—Labia and maxillae of male holotype of species of *Pycnothele*, ventral views: *P. auronitens* (= *P. auripilus* = *A. modestus* [in part]); 17, *P. perdital*; 18, *P. singularis* (= *A. singularis* = *A. modestus* [in part]). Arrows show cuspules.

Genus *Pycnothele* (Chamberlin, 1917)

Pycnothele Chamberlin, 1917:26; Mello-Leitão 1923:39; Petrunkevitch 1928:73; 1940:303; Berland 1932:329; Gerhardt & Kaestner 1939:591; Neave 1940:1051; Roewer 1942:275; Schiapelli & Gerschman 1942:319; Schiapelli & G. de Pikelin 1965:15; 1967:53; G. de Pikelin & Schiapelli 1970:100; Bonnet 1958:3836; Pérez-Miles & Capocasale 1983:2; Raven 1985:100.

Trechona: Keyserling 1891:16 (in part).

Crypsidromus: Simon 1903:931 (in part); Bücherl 1952:132 (in part).

Metriopelma: Pocock 1903:112 (in part); Mello-Leitão 1923:168 (in part); Bonnet 1957:2826 (in part).
Androthelopsis Mello-Leitão, 1934:402; Roewer 1942:217; Bonnet 1955: 322; Raven 1985:101. NEW SYNONYMY.
Heteromma Mello-Leitão, 1935:356 (preoc. by *Heteromma* Menge 1856, in Neave 1939:640); Bonnet 1957:2184.
Agersborgia Strand, 1936:167 (new name for *Heteromma*); Bonnet 1955: 205.
Pycnothelopsis Schiapelli & Gerschman, 1942:319; Schiapelli & G. de Pikelin 1965:15; 1967:59; Bücherl 1957:408; Capocasale & Pérez-Miles 1979:1 (in part); Pérez-Miles & Capocasale 1982:1 (in part); 1983:1.

Diagnosis.—*Pycnothele* differs from other Pycnothelinae because the males possess bulbs with differentiated short emboli and subapical wide vanes (Figs. 7-15); in females, spermathecae each have a long and narrow neck gradually widening apically; fundus subglobulose.

DISCUSSION

Schiapelli & Gerschman (1942) established the separation between *Pycnothele* and *Pycnothelopsis* according to the following characters: scopulae extension on metatarsi I and II, labial and maxillary cuspulae and ocular dimensions. Capocasale & Pérez-Miles (1979) and Pérez-Miles & Capocasale (1982, 1983) invalidated some characters considered as diagnostic in these genera, although they maintained them as separate taxa.

Raven (1985:101) established the synonymy between *Pycnothelopsis* and *Androthelopsis*, maintaining the species under study in two separate genera: *Pycnothele* and *Androthelopsis*. This author based the separation on the following characters: integral/pseudosegmented tarsi and height of vanes on bulb.

According to the preceeding analysis, the characters considered as diagnostic of *Pycnothele* and *Androthelopsis* have no value. The mentioned differences between these genera are either erroneous or do not justify that they be maintained as separate taxa.

Proper synapomorphies of each genus that can justify their separate existences as monophyletic groups were not found. Raven (1985:45) indicated that wide vanes on the bulb are a synapomorphy of *Pycnothele* plus *Androthelopsis* (sister groups). We agree with this author in the polarity assigned to the character, but we consider that it is a synapomorphy of generic level, which indicates the monophyly of the species attributed to both genera. Using similarity criteria, bulb morphology and embolus length are more similar among the species attributed to *Pycnothele* and *Androthelopsis* than they are between any of these species and the other members of the Pycnothelinae.

A significant morphological discontinuity observed among the species attributed to *Pycnothele* and *Androthelopsis* involved the character, entire/divided scopulae of tarsi IV. This character has been traditionally used to separate genera in Mygalomorphae. If only this character is considered, the species would be placed in two genera; (1) *Androthelopsis* plus *P. auronitens*, with divided scopula and (2) *Pycnothele* (monospecific). But since divided scopulae on tarsi IV are plesiomorphic, *Androthelopsis* plus *P. auronitens* would constitute a genus based on symplesiomorphy. If *Pycnothele* remained as a monospecific genus and sister group of *Androthelopsis* (*sensu* Raven 1985), both

taxa would be paraphyletic (*sensu* Platnick 1976). Other morphological discontinuities justifying the existence of *Pycnothele* and *Androthelopsis* as separated genera were not found.

The results obtained have induced us to establish the synonymy between *Pycnothele* and *Androthelopsis*. *Pycnothele* (valid name for priority ICZN, art. 23) would be based on the following synapomorphy: wide and conspicuous subapical vanes on bulb (Figs. 7-15).

KEY TO SPECIES OF THE GENUS *PYCNOTHELE*

Males

1. Scopulae entire on tarsi IV (Fig. 3).....*P. perdit*
Scopulae on tarsi IV, divided by a stripe of thicker and longer setae.....2
- 2.- Bulbal duct presenting a strong subterminal curvature basally (Figs. 7, 10, 13)*P. auronitens*
Bulbal duct without such curvature (Figs. 8, 11, 14)*P. singularis*

Pycnothele auronitens (Keyserling, 1891)

Figs. 1, 2, 7, 10, 13, 16

Trechona auronitens Keyserling, 1891:16.

Metriopelma auronitens: Pocock 1903:114; Mello-Leitão 1923:173; Petrunkevitch 1939:279; Bonnet 1957:2826; 1959:4680.

Crypsidromus auronitens: Simon 1903:931; Bücherl 1952:132.

Psalistops auripilus Mello-Leitão, 1946:8. NEW SYNONYMY.

Pycnothelopsis modestus: Schiapelli & G. de Pikelin 1971:61 (in part).

Pycnothelopsis auripilus: Capocasale & Pérez-Miles 1979:3 (in part); Pérez-Miles & Capocasale 1982:1.

Pycnothelopsis auronitens: Pérez-Miles & Capocasale 1983:2.

Androthelopsis modestus: Raven 1985:102 (in part). NEW SYNONYMY.

Pycnothele auronitens: G. de Pikelin & Schiapelli 1970:100; Raven 1985:100.

Diagnosis.—*P. auronitens* differs from *Pycnothele perdit*, by the scopula on tarsus IV which is divided by a stripe of longer setae; from *P. singularis* by the strong proximal curvature of the bulb duct tract (visible in ventral and prolateral views) (Figs. 10-13).

Description.—*Male* ($N=4$): Carapace, length: 5.6-7.2 mm (mean = 6.28 ± 0.73 SD), width: 4.4-5.1 mm (mean = 4.75 ± 0.35 SD). Fovea procurved. Chelicerae without rastellum, intercheliceral tumescence present. Ocular tubercle well defined, longer than wide; AME: 0.18-0.25 mm (mean = 0.11 ± 0.03 SD); ALE: 0.20-0.30 mm (mean = 0.26 ± 0.04 SD); PME: 0.15-0.20 mm (mean = 0.18 ± 0.03 SD); PLE: 0.23-0.35 mm (mean = 0.28 ± 0.05 SD). Labium with 3-5 cuspules. Maxillae subrectangular, distal prolateroventral lobe pronounced, proximal prolateroventral lobe with numerous cuspules. Tibial apophysis absent. Tarsi without spines, with two bipectinated claws. Scopulae on tarsi I-III entire, on tarsi IV divided in half by a longitudinal stripe of longer setae. Apical scopulae on metatarsi I and II; III and IV without scopulae. Sternal sigilla marginal. Anterior spinnerets monoarticulated, short; posterior spinnerets triarticulated, apical segment short and domed. Palpal bulb pyriform with

subapical wide vanes, embolus differentiated, short; duct-tract of bulb presenting a strong subterminal curvature proximally (visible in ventral and prolateral views).

Discussion.—This species was placed in *Pycnothele* by G. de Pikelin & Schiapelli (1970). *Psalistops auripilus* (Mello-Leitão, 1946), was transferred to *Pycnothelopsis* by Schiapelli & G. de Pikelin (1971) (not by Capocasale & Pérez-Miles (1979), as Raven said (1985:102)) and placed in the synonymy of *P. modestus*. Capocasale & Pérez-Miles (1979) separated this synonymy into two species: *Pycnothelopsis auripilus* and *Pycnothelopsis modestus*. Pérez-Miles & Capocasale (1983) transferred *P. auronitens* to *Pycnothelopsis* establishing the specific synonymy *P. auronitens* = *P. auripilus*. Raven (1985) did not accept this synonymy and placed *P. auronitens* back in *Pycnothele* and *P. auripilus* in *Androthelopsis*. He based the change on the fact that *P. auronitens* shares with *Pycnothele*: (1) the absence of pseudosegmented tarsi in the male and (2) elevated vanes on the bulb. The first character state is at odds with his own statement that tarsi I and II of male *Pycnothele* are pseudosegmented. In any case, both characters became useless as a result of the present analysis. In our present study important differences were not found between the types of *P. auronitens* and *P. modestus*. This confirms the specific synonymy established by Pérez-Miles & Capocasale (1983).

The synonymy established again by Raven (1985) between *A. modestus* (= *P. singularis*) and *P. auripilus* (= *P. auronitens*) is overturned. These species are distinguished by the characters mentioned in the diagnosis which agree with the results obtained by Capocasale & Pérez-Miles (1979).

Material examined.—**BRAZIL:** Rio Grande, Taquara, holotype male of *Pycnothele auronitens* (BMNH). **URUGUAY:** Lavalleja, Arequita (C. de Zolessi) 1 male (MNHN); Maldonado, Sierra de las Animas (Pérez, Delgado) 1 male (MNHN); Florida, holotype male of *Psalistops auripilus* (MNHN).

Pycnothele perdita Chamberlin, 1917

Figs. 3, 4, 9, 12, 15, 17

Pycnothele perdita Chamberlin, 1917:26; Roewer 1942:275; Bonnet 1958:3836; Schiapelli & Gerschman 1942:319; Schiapelli & G. de Pikelin 1965:15; 1967:54; Pérez-Miles & Capocasale 1983:2; Raven 1985:100. *Pycnothele perditus* (sic): Mello-Leitão 1923:40; Petrunkevitch 1928:73; Schiapelli & G. de Pikelin 1967:48.

Diagnosis.—Males of *P. perdita* differ from other *Pycnothele* species by their entire scopulae on tarsi IV and by their bulb morphology (Figs. 9, 12, 15).

Description.—*Male:* Carapace, length: 14.5 mm; width: 12.2 mm. Fovea procurved. Chelicerae without rastellum, intercheliceral tumescence present. Ocular tubercle well defined, longer than wide; AME: 0.75 mm; ALE: 0.50 mm; PME: 0.28 mm; PLE: 0.50 mm. Labium with 3 cuspules (2 visible plus a base). Maxillae subrectangular, distal prolateroventral lobe pronounced, proximal prolateroventral lobe with numerous cuspules. Tibial apophysis absent. Tarsi without spines, with two bipectinated claws. Scopulae on tarsi I-IV entire. Apical scopulae on metatarsi I and II; III and IV without scopulae. Sternal sigilla marginal. Anterior spinnerets monoarticulated, short; posterior spinnerets triarticulated, apical segment short and domed. Palpal bulb pyriform with subapical wide vanes; embolus differentiated, short; duct tract of bulb gently curved in ventral view (Fig. 15).

Female: Carapace length: 17 mm; width: 13 mm; AME: 0.54 mm; ALE: 0.51 mm; PME: 0.20 mm; PLE: 0.51 mm. Labium with 1 cuspule. Scopulae on tarsi I and II entire; III and IV divided. Spermathecae with long and narrow neck, gradually widening apically, fundus subglobulose. Other characters as in male.

Material examined.—**BRAZIL**: Rio Parahyba, holotype male and paratype female (MCZ).

Pycnothele singularis (Mello-Leitão, 1934) NEW COMBINATION

Figs. 5, 6, 8, 11, 14, 18

Androthelopsis singularis Mello-Leitão, 1934:402; Roewer 1942:217; Bonnet 1955:322; Raven 1985:101.

Pycnothelopsis modestus Schiapelli & Gerschman, 1942:319 NEW SYNONYMY; Schiapelli & G. de Pikelin 1965:15; 1967:59; 1971:61 (in part); Bücherl 1957:405; Capocasale & Pérez-Miles 1979:4; Pérez-Miles & Capocasale 1982:1; 1983:4; Brignoli 1983:142.

Androthelopsis modestus: Raven 1985:102 (in part) NEW SYNONYMY.

Diagnosis.—*P. singularis* differs from *P. perdita*, by having the scopulae on tarsi IV divided; and from *P. auronitens*, by the tract of bulb which lacks subterminal curvature (Figs. 8, 11, 14).

Description.—*Male* ($N=6$): Carapace, length: 6.1–11.0 mm (mean = 8.23 ± 1.75 SD), width: 4.6–7.5 mm (mean = 6.43 ± 1.05 SD). Fovea procurved. Chelicerae without rastellum, intercheliceral tumescence present. Ocular tubercle, well defined, longer than wide; AME: 0.18–0.30 mm (mean = 0.24 ± 0.04 SD); ALE: 0.23–0.35 mm (mean = 0.30 ± 0.05 SD); PME: 0.15–0.30 mm (mean = 0.22 ± 0.05 SD); PLE: 0.20–0.35 (mean = 0.29 ± 0.06 SD). Labium with 1–4 cuspules. Maxillae subrectangular, distal prolateroventral lobe pronounced, proximal prolateroventral lobe with numerous cuspules. Tibial apophysis absent. Tarsi without spines, with two bipectinated claws. Scopulae on tarsi I–III entire, scopulae on tarsi IV divided by a longitudinal stripe of longer setae. Apical scopulae on metatarsi I and II; III and IV without scopulae. Sternal sigilla marginal. Anterior spinnerets triarticulated; apical segment short, domed. Palpal bulb pyriform with subterminal wide vanes; embolus differentiated, short; duct-tract of bulb gently curved in ventral view (Fig. 11).

Discussion.—*P. modestus* was transferred to the genus *Androthelopsis* by Raven (1985:101) who maintained it as a different species from *A. singularis*. In the type comparison, except for slight differences in size, other important differences in the characters studied were not found. This is the basis of the specific synonymy here established. As a result of the generic synonymy (*Pycnothele* = *Androthelopsis*), the name *Pycnothele singularis*, must prevail by priority (ICZN, art. 23).

The synonymy established between *A. modestus* (= *P. singularis*) and *P. auripilus* (= *P. auronitens*) by Raven (1985:161) is considered incorrect. These species are differentiated by the characters indicated in the diagnosis.

Material examined.—**BRASIL**: SÃO PAULO; Alto da Serra, holotype male of *Androthelopsis singularis* (IB). **ARGENTINA**: SANTIAGO DEL ESTERO; Colonia Dora (Prosen), holotype male of *Pycnothelopsis modestus* (MACN); CÓRDOBA (Mansilla) 1 male (MACN); CHACO; Colonia Benítez, 1 male (MACN); ENTRE RÍOS; Paraná, 1 male (MACN). **URUGUAY**: CERRO LARGO; Río Tacuarí (Costa; Pérez) 1 male (MNHN); ARTIGAS; Cerro del Zorro (Gudynas; Skuk) 1 male (MNHN); Arroyo de la Invernada, 1 male (MNHN); SALTO, Río Arapey (Shanon) 2 males (MNHN).

UNCERTAIN SPECIES OF *PYCNOTHELE*

Heteromma anomala Mello-Leitão, 1935:356. Holotype male from Brazil, Rio de Janeiro (IB) examined. According to the morphology of the bulb, we agree with Raven (1985) who placed this species in *Pycnothele* (next to *P. perdita*). However, (1) it has no cuspules on the labium and (2) tarsi IV are absent in the holotype. Mello-Leitão (1934) did not say if the scopulae on tarsi IV are entire or divided. For these reasons, at present, it is not possible to reach a conclusion and it can only be considered as unidentifiable.

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BEHAVIORAL FLEXIBILITY IN ORB WEB CONSTRUCTION: EFFECTS OF SUPPLIES IN DIFFERENT SILK GLANDS AND SPIDER SIZE AND WEIGHT

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ABSTRACT

Comparisons of webs spun in the field when both sticky and non-sticky silk supplies were complete, when both were recently depleted, and when only non-sticky supplies were depleted show that *Leucauge mariana* and *Micrathena sexspinoso* vary design features of their orbs such as numbers of radii and sticky spiral loops, web area and proportion covered with sticky spiral, sticky spiral symmetry, and spaces between sticky spiral loops in response to changes in the amounts of both sticky and non-sticky silk that they have available. Spider size, spider weight and possibly website also influence *L. mariana* web designs.

INTRODUCTION

The orbs of araneid spiders are composed of a sticky spiral, produced by the aggregate and flagelliform glands, and a network of non-sticky supporting lines (radii, frames, hub and temporary spiral) drawn from the ampullate glands (Kovoor 1977; Kavanagh and Tillinghast 1979). Several aspects of orb web design have been thought to be species- or genus-specific (Savory 1952; Witt and Baum 1960; Reed and Jones 1965; Witt et al. 1968; Risch 1977; Foelix 1982; Ramousse and LeGuelte 1984; Tyshchenko 1984). Individual spiders appear however, to adjust some web characteristics on the basis of their silk supply. Laboratory experiments using drugs that stimulated non-sticky silk production altered orb sizes and designs (Witt et al. 1968), as did manipulation of non-sticky silk production by altering the spider's demands for non-sticky silk (Reed et al. 1970). These studies did not take into account, however, other possible effects of the drugs, or possible effects of changes in silk supplies in other glands. The present report of field observations of the araneids *Leucauge mariana* (Keyserling) and *Micrathena sexspinoso* (Hahn) shows that recent expenditure of sticky as well as non-sticky silk influences web designs. Spider size, spider weight and possibly websites are also shown to influence web design in *L. mariana*.

MATERIALS AND METHODS

Individual spiders were followed during the course of a day by marking websites rather than spiders, as spiders were generally several meters from each

other, and usually did not change sites during the day (spiders that did move were not included). *L. mariana* was observed in second growth near San Antonio de Escazu, San José Province, Costa Rica, and *M. sexspinoso* at the edge of a large clearing at the La Selva field station near Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica. All individuals observed were mature females. Webs were measured in the field, and then collapsed by cutting all but three radii near their outer ends with a scissors, leaving all silk still in the web, and the frame and anchor lines intact. Web area was estimated by multiplying vertical length times horizontal width measured from frame to frame. By weighing paper cutouts of 53 photographed *L. mariana* webs, it was determined that such estimates correlate strongly with area ($r = 0.80$). The number of sticky loops was the average of the number above and below the hub in *M. sexspinoso*, and the average of those above, below, and to the right and left of the hub in the less symmetrical webs of *L. mariana*. The average space between sticky spiral loops was the distance from the inner to the outer loop divided by the number of loops.

Those *L. mariana* spiders which were to be weighed were placed in individual plastic vials with fresh leaves within 1-2 hours of finishing their first webs of the day, and weighed to the nearest 0.1 mg less than 12 hours later on an electrical balance. Using the average rate of weight loss for nine spiders kept in vials for seven hours (0.05 mg/h—spider weights averaged about 45 mg), each spider's estimated weight when it spun its web was calculated. Each spider was placed in alcohol after being weighed, and cephalothorax and tibia I lengths were measured later using a dissecting microscope.

Website effects on orb design were investigated by measuring the first webs of the day for a series of spiders. These spiders were then removed (with little or no damage to the webs) and were replaced the same morning by other spiders taken from finished orbs of their own; the first webs made by the replacement spiders at the same sites were measured the next morning.

When possible, statistical tests were performed comparing different webs spun by the same spider on the same day and at the same site, allowing the spider to act as its own control.

RESULTS

Normal webs.—Both *L. mariana* and *M. sexspinoso* replaced damaged webs 1.5-10 hours after their original webs were destroyed at 0700-0900 hours. The second, replacement webs of both species were consistently smaller in area, had fewer radii, and fewer loops of sticky spiral (Table 1). The average spaces between sticky spiral loops were unchanged. Third webs of *L. mariana* spun the same day to replace destroyed second webs (all third webs were built <15 hours after the first web) showed further reductions in numbers of radii and loops, increased spaces between loops, but no further change in web area (Table 1).

The relative portion of *L. mariana* webs within the outermost loop of sticky spiral also varied. The distances from the outermost sticky loops to the outer ends of the radii were greatest in third, smaller in second, and smallest in first webs (Fig. 1) (first and second webs differed comparing numbers of distances both <0.6 cm and >1.5 cm with Chi Square— $p < 0.05$, $p < 0.001$ respectively); second and third differed comparing both <1.1 and >2.0 cm—both $p < 0.001$ with Chi Square).

Table 1.—Averages and standard deviations of characteristics of normal first, second and third webs and experimental second webs, and statistical comparisons of ratios from webs spun by the same spiders on the same days at the same sites (two sets of first webs are used in the comparisons of *L. mariana* webs). Differences between values followed by the same letter are highly significant ($p < 0.001$) with Mann-Whitney *U*-test.

| Web | Number of Radii | Number of Sticky Loops | Area (cm) ² | Space Between Loops (cm) | N |
|-----------------------------|-----------------|------------------------|------------------------|--------------------------|-----|
| <i>Micrathena sexspinos</i> | | | | | |
| First | 38.3 ± 7.1 | 25.0 ± 6.5 | 367 ± 190 | 0.23 ± 0.04 | 121 |
| Second | 26.2 ± 4.4 | 19.3 ± 4.6 | 286 ± 101 | 0.24 ± 0.04 | 50 |
| Experimental | 32.0 ± 4.6 | 24.3 ± 4.5 | 416 ± 148 | 0.25 ± 0.06 | 37 |
| Second/First | 0.66 ± 0.16a | 0.75 ± 24 | 0.80 ± 31b | 1.06 ± 0.15 | 45 |
| Exptl. / First | 0.83 ± 0.09a | | 1.09 ± 0.31b | | 35 |
| <i>Leucauge mariana</i> | | | | | |
| First | 30.2 ± 3.3 | 41.2 ± 10.2 | 670 ± 222 | 0.23 ± 0.03 | 80 |
| Second | 23.4 ± 2.7 | 27.4 ± 4.9 | 453 ± 250 | 0.24 ± 0.04 | 78 |
| Third | 20.7 ± 3.0 | 22.3 ± 4.5 | 403 ± 150 | 0.26 ± 0.07 | 40 |
| Experimental | 26.2 ± 3.4 | 35.5 ± 7.2 | 549 ± 255 | 0.22 ± 0.04 | 29 |
| Second / First | 0.79 ± 0.11c | 0.70 ± 0.14d | 0.64 ± 0.18 | 1.01 ± 0.13e | 40 |
| Third / First | 0.62 ± 0.12c | 0.53 ± 0.14d | 0.65 ± 0.20 | 1.24 ± 0.25e | 40 |
| Second / First | 0.82 ± 0.08f | 0.67 ± 0.09 | 0.68 ± 0.19g | 1.05 ± 0.14 | 29 |
| Exptl. / First | 0.92 ± 0.07f | | 0.96 ± 0.28g | | 29 |

Sticky spiral asymmetry was reduced in second and third *L. mariana* orbs. Absolute values of differences between the average number of loops and the numbers of loops in the four sectors were summed for each web in 44 cases in which the same spider made three successive webs at the same site on the same day. The sums for first webs ($\bar{x} = 8.4 \pm 5.0$) were larger than those in second ($\bar{x} = 5.0 \pm 4.6$) and third ($\bar{x} = 4.4 \pm 4.2$) webs (both $p < 0.001$ with Mann-Whitney *U*-test). In addition, when the difference between the maximum and minimum number of loops in each web were compared between first, second and third webs, those in first webs ($\bar{x} = 5.8 \pm 3.3$) were larger than those in second ($\bar{x} = 3.4 \pm 3.2$) and third ($\bar{x} = 3.0 \pm 2.7$) webs (both $p < 0.001$ with Mann-Whitney *U*-test), and the proportion of webs with differences of >4 loops was greater among first than in second or third webs (both $p < 0.001$ with Chi Square). Since spiders often reused frame lines from previous webs, the sticky spirals of later orbs may have been more symmetrical because these webs tended to have relatively larger frame areas as compared to sticky spiral areas, making fewer turnbacks in the sticky spiral necessary (Eberhard 1969).

Experimental modification of relative amounts in glands.—The relative amounts of sticky and non-sticky silk available to the spider when the second web was begun were modified experimentally by allowing the spider to finish adding non-sticky lines to the first web (radii, frame, hub, temporary spiral), but then cutting the radii as above, thus preventing the spider from laying any sticky silk. The spider's non-sticky silk supply was thereby reduced, while the sticky silk supply was left intact. The experimental second webs that followed did not have reduced areas; they had fewer radii and, in *L. mariana*, fewer sticky loops than first webs, but the reductions in both were significantly less than those in normal second webs of both species (Table 1). The relative portion of the web enclosed within the outermost sticky spiral loop was not reduced as in normal second webs

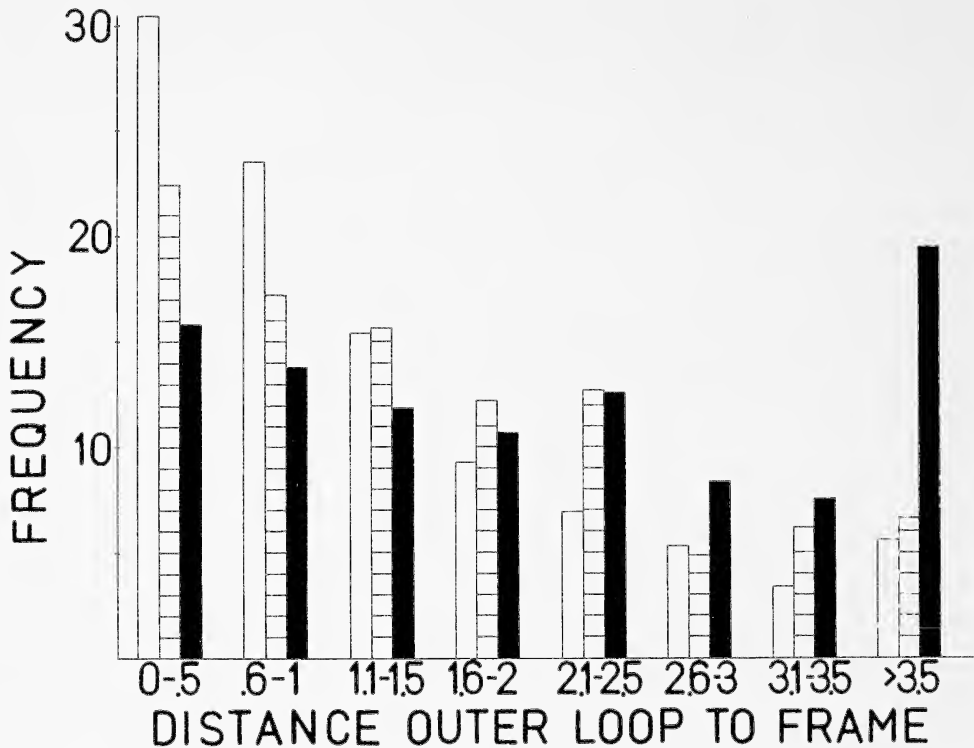


Fig. 1.—Frequencies of distances between outer loops of sticky spiral and ends of radii in normal first (white), second (hatched) and third (black) webs ($N = 44$ in each case) that were spun by *L. mariana* females (three webs/female, all on the same day). Distributions are significantly different with Chi-Square Test.

(predicted distances from outer loops were calculated for experimental webs using the percentages for normal second webs in Fig. 1).

By cutting radii as soon as they were laid, *L. mariana* spiders were experimentally induced to lay more than one additional set of radii during construction of replacement webs (radii represent approximately 20-30% of the non-sticky silk in a finished orb—Eberhard 1986), confirming that orb construction of normal second webs does not completely empty the ampullate glands of this species, just as in the first webs of *Araneus diadematus* Clerck (König 1951; Witt et al. 1968), *L. mariana* and *Gasteracantha cancriformis* (Linnaeus) (Eberhard 1986), and the unidentified araneid studied by Hingston (1920).

Correlations with spider size and weight.—Correlations between spider size and weight and dimensions of first webs of 138 *L. mariana* showed that larger and heavier spiders made webs with more closely spaced sticky spiral loops, and somewhat larger webs (Table 2). Partial correlations showed that both weight and a combination of body size measures ($x = \text{tibia} / \text{average tibia} + \text{cephalothorax} / \text{average cephalothorax}$) had significant correlations with sticky spiral spacing (partial correlation coefficients were -0.26 and -0.23 respectively, both $p < 0.001$). Partial correlations with web area were not significant.

Website effects.—There were strong positive correlations between the slants and areas of successive webs at the same site spun by different spiders ($r = 0.46$, $p <$

Table 2.—Correlation coefficients between web and body measurements of 138 adult female *Leucauge mariana* (* $p < 0.05$, ** $p < 0.001$).

| | Area | Number Sticky Loops | Space between Sticky Loops | Number Radii | Slant |
|---------------|---------|------------------------|-------------------------------|-----------------|--------|
| Cephalothorax | 0.206* | −0.065 | −0.358** | −0.056 | −0.124 |
| Tibia | 0.172 | −0.100 | −0.343** | −0.027 | −0.055 |
| Wet weight | 0.267** | 0.033 | −0.399** | 0.006 | −0.117 |

0.001 and $r = 0.335$, $p < 0.01$ respectively for 63 pairs of webs). Other web features showed no significant relationships, nor was there a significant correlation between the weights of successive spiders occupying the same sites.

DISCUSSION

It might be thought that differences between first and second webs were due to the first webs usually being spun in darkness and the second in daylight (Ramousse and LeGuelte 1979 on *Araneus diadematus*). The differences between second and third webs of *L. mariana* and experimental and second webs of both species (all built during the day) indicate however that light conditions during construction do not explain the changes in design.

The reduced numbers of radii in both normal and experimental second orbs of *L. mariana* and *M. sexspinosa* suggest that, as in *A. diadematus*, non-sticky silk in the ampullate glands probably influences their web designs. The experimental webs show, however, that the supply of sticky silk can partially "over-rule" the effect of non-sticky silk availability. *A. diadematus* may also respond to cues from its sticky silk glands. Preliminary evidence shows similar reductions may occur in radius and sticky spiral loop number and web area when webs are built in close temporal succession (Ramousse 1977). Slight reductions of numbers of sticky spiral loops occurred in webs spun by spiders which had been milked of non-sticky silk, but prevented from laying sticky silk for three weeks (presumably gland output was reduced when demand ceased) as compared with controls which had spun normal webs (21.0 vs. 26.5, $N = 6$ for both, significance levels were not given) (Reed et al. 1970).

Sticky silk forms a large fraction of an orb. Its length ranged from about 36 to 54% of the total length of silk in more or less typical orb designs (Eberhard 1986). By weight it may be an even larger fraction. The non-sticky scaffolds of *Argiope aurantia* webs weighed only about 16% of the dry weight of the finished orb (Tillinghast et al. 1984). Taking into account the non-sticky stabilimentum, which was included along with the sticky spiral in the remaining 84%, it is probable that the sticky lines account for 70-80% of the dry weight of an orb (E. K. Tillinghast, pers. comm.). Sticky silk is also, of course, a key web component in trapping prey. In sum, it is perhaps not surprising that the supply of sticky silk influences web design. The relatively smaller portions of later webs occupied by sticky spiral, the big proportion occupied in experimental second webs, and the spiders' ability to lay many extra radii during second web construction all suggest that sticky rather than non-sticky silk sometimes limits web size (see also Eberhard 1986).

It is tempting to postulate that non-sticky gland contents determine the design of non-sticky web components, and sticky silk supplies affect sticky silk design features. There are, however, probably "crossovers" in cues from the two types of glands; for instance, web area (a design feature of non-sticky lines) was not reduced in experimental second webs of either species, even though supplies of non-sticky silk had been reduced.

Individual araneids sometimes produce non-sticky lines with varying diameters (e.g., Christiansen et al. 1962; R. W. Work pers. comm.), and the sizes and spaces between sticky balls on the sticky spiral of *L. mariana* webs varies substantially even within a single web (Eberhard unpub.). Thus the web measurements given here may not accurately reflect total amounts of material in different webs. The probable trend in diameter modification (smaller diameters when gland less full) suggests that the trends documented here give underestimates of the differences in the amount of material in successive webs.

Several previous studies have analyzed the relationships between spider size and weight, but many comparisons include the possibly confounding effects of species or age (instar) differences. Comparisons of webs of conspecific mature females with different weights (Christiansen et al. 1962; Risch 1977) and different body sizes (Risch 1977) suggest that both factors have effects on web design in other araneid species. Variations in *L. mariana* web designs associated with greater spider weight were similar to those associated with relatively greater supplies of sticky silk (decreased spaces between sticky loops, greater area), but differed in showing no relations with numbers of radii or sticky loops (Table 1). Larger spider weights might be associated to some extent with greater recent feeding success and thus, presumably, greater amounts of material in the glands, but a female spider's weight is probably largely determined by the stage of development of its eggs. Thus the weight effects documented here may be largely independent of the gland-filling effects.

Website may be still another factor causing *L. mariana* web designs to vary. Spiders often reuse some of the frame lines from previous webs (Eberhard, unpub.), and the correlations in slant and area of successive first webs could be due to frame reuse. It is also possible that other website characteristics were important. Adjustments of web design to local conditions are undoubtedly advantageous for orb weavers; they are suggested by field data (Leborgne and Pasquet 1987), and have been documented in confinement (Tilquin 1942; Szlep 1958; LeGuelte 1966).

The intraspecific variations documented here are substantial. For instance, even when one controls for possible effects of spider size, weight, and website in *L. mariana*, first webs average 146% more radii, 185% more sticky spiral loops, and 166% more area than third webs; some individual spiders, of course, showed even greater variations. The magnitude of this variation, the existence of similar variation in other species (Ramousse and LeGuelte 1979; Leborgne and Pasquet 1987), and the correlations between these and other web characters (Leborgne and Pasquet 1987) weaken the old hope that orb designs can provide reliable species-specific characters (e.g., Savory 1952; Foelix 1982). If such web characters exist, they may be associated with more subtle details such as number and pattern of hub loops, relative size of free zone, etc. (see Coddington 1986 for examples of useful generic characters in webs of Theridiosomatidae). It is possible that different species have different ways of adjusting to changes in factors such as

supplies of sticky and non-sticky silk and spider size and weight, but proof of this will require much more information that is presently available. Intraspecific variation seen in other studies (LeGuelte 1966; Risch 1977; Ramousse and LeGuelte 1979, 1984; Nentwig 1983, 1985; Tyschenko and Marusik 1985, Tyshchenko et al. 1985; Buskirk 1986; Leborgne and Pasquet 1987) may be due at least in part to the factors discussed here.

In light of these findings, the probable nervous mechanisms controlling orb construction appear to be extraordinarily complex. Both internal factors (weight, body size, contents of sticky and non-sticky silk glands) and external factors (website and/or previous lines present there) are integrated in determining a variety of design features, ranging from basic characteristics such as numbers of radii and sticky loops and web area, to more subtle aspects such as the relative symmetry of the sticky spiral and the relative fill of the web area with sticky spiral. Different features are modified at least partially independently. The influence of gland contents and perhaps that of the website may incorporate feedback loops involving amounts of silk and web designs used previously (Reed et al. 1970; Tillinghast and Townley 1986; this study). During actual construction several other factors, such as gravity, leg length and distances and angles between lines, and memories of distances and directions travelled (Hingston 1920; Tilquin 1942; LeGuelte 1966; Vollrath 1986, 1987; Eberhard 1987, 1988) also influence the paths taken and the lines laid. The reasons why spiders opt for different orb designs when they have different amounts of silk available are not yet clear; but there is no doubt that we must discard once and for all the old image of orb weaving spiders spinning out the same rigidly programmed, inflexible geometric patterns in their webs day after day.

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ORB WEB RECYCLING IN *ARANEUS CAVATICUS* (ARANEAE, ARANEIDAE) WITH AN EMPHASIS ON THE ADHESIVE SPIRAL COMPONENT, GABAMIDE

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ABSTRACT

The feeding of radiolabeled conspecific orb webs to *Araneus cavaticus* Keyserling clearly demonstrated the ability of this species to solubilize nearly all of the orb web, although in no instance was complete solubilization achieved. A principal component of the nonsolubilized portion is probably minor ampullate silk, as spiders fed pulled minor ampullate silk were unable to solubilize the majority of the samples. In contrast, spiders were able to completely solubilize pulled major ampullate silk. Despite the overall high percentage of web solubilization, the recycling efficiencies obtained, while variable, were never in excess of 32% (as determined using webs built by spiders fed ¹⁴C-glucose).

A complete assessment of web recycling will have to consider the fate of ingested low molecular weight adhesive spiral components as well as web proteins. Of those components which have been identified, only GABamide was followed in the present study due to the labeled compound fed. On average ingested GABamide appears to be more quickly reincorporated into new web than ingested protein residues and this reutilization is, for the most part at least, in the form of GABamide. From spiders which did not build webs until several days after being fed orb webs, the indication is that GABamide can be stored for future web construction for such a length of time. Whether any storage is by physical separation from agents with metabolic activity against GABamide or by a degree of metabolic inertness is unknown.

INTRODUCTION

In previous studies the digestive fluid of *Argiope aurantia* Lucas was found to be capable of solubilizing all orb web adhesive spiral, radial, and junctional components except minor ampullate fibers (Tillinghast and Kavanagh 1977; Kavanagh and Tillinghast 1979), which commonly accompany major ampullate fibers in radii (Kavanagh and Tillinghast 1979; Work 1981). However, the method employed to make this determination, that of applying filter discs wetted with digestive fluid to plated webs, produced results which, upon reflection, could have been open to misinterpretation. The act of removing the filter disc after the incubation period could have resulted in the simultaneous removal of underlying web components which may have been only partially solubilized or otherwise weakened by the digestive fluid, rather than completely solubilized. Additionally, in no instance was web completely solubilized when immersed in a buffered solution containing digestive fluid (Tillinghast and Kavanagh 1977), and it seemed unlikely that minor ampullate fibers alone could account for all of the nonsolubilized portion. This incomplete solubilization also made the extremely

high recycling efficiency reported by Peakall (1971) seem unlikely. In an effort to resolve these inconsistencies we have examined orb web digestion and recycling *in vivo*. The ability to procure individually samples of major ampullate and minor ampullate silk also allowed us to examine more specifically the digestion and, for the former silk type, recycling of these orb web components. It should be noted that while a fraction of the ingested web components was undoubtedly used for purposes not directly related to web construction, but was nevertheless recycled in a denotative sense, in this paper the term "recycle" is restricted to the utilization of those components in subsequent webs or silks.

MATERIALS AND METHODS

Adult and penultimate female and male *Araneus cavaticus* Keyserling were collected in southern New Hampshire and Maine and kept either in cages (Tillinghast and Kavanagh 1977) or small vials, depending on whether web construction was desired or not.

To obtain radioactive major ampullate silk, spiders were fed from 4 to 20 μCi D- $^{14}\text{C}(\text{U})$ glucose (sp. act. 4.28 mCi/mmol or 329 mCi/mmol, New England Nuclear®; or 263 mCi/mmol, ICN® Radiochemicals). The silk was mechanically drawn one and/or two days after feeding as described previously (Tillinghast et al. 1984), except that a pulling rate of 1.0 cm/s was used. Again, the silking operation was monitored frequently with the aid of an Olympus®, Model X-Tr, stereo dissecting microscope, to insure as much as possible a collection of major ampullate silk free from pyriform, aciniform, and minor ampullate fibers. Since the aggregate and flagelliform glands of males degenerate shortly after adulthood is reached (Sekiguchi 1955a,b), making adhesive spiral and, thus, orb web construction impossible, adult males were only used for this purpose.

The silk pulled from each spider was cut into two portions, one roughly three times the size of the other. Each portion was desiccated over CaSO_4 and NaOH *in vacuo* and their dry weights were measured on a Perkin-Elmer® AD-2 autobalance. The smaller portions were hydrolyzed in 6N HCl at 110°C for 24 h, with the hydrolysates being used to determine specific activity. Radioactivity was measured in a Beckman® Beta-Mate II scintillation counter using Beckman® Ready-Solv EP as the scintillation fluid, and amino acids were quantitatively measured by the method of Moore (1968). The larger portions were assumed to have the same specific activities as their smaller counterparts.

Radioactive whole orb webs were obtained from spiders fed 10 μCi D- $^{14}\text{C}(\text{U})$ glucose (sp. act. 263 mCi/mmol, ICN®) each. After collecting the webs on 20 μL micropipettes, each was scraped off as a ring with a new razor blade and cut into one large and one small piece. These pieces were treated the same as the pulled major ampullate silk above.

Nonradioactive spiders were fed radioactive pulled silk or whole web in one of two ways. Either the spiders were offered the radioactive material while pinioned or it was placed in the spider's nonradioactive web. For the former method the spider was temporarily anesthetized with CO_2 and taped down, allowing close scrutiny of the external digestion process when the above dissecting microscope was used. For the latter method, all but two opposing frame lines were cut following placement of radiolabeled material in the unlabeled web. This was done

both to encourage web recycling and to insure that none of the radioactive material, particularly the pulled silk, would be lost during the spider's recycling of the web. The greater freedom of movement permitted by this method created a more normal situation. It was more difficult or impossible, however, to observe the movements of the spider's mouthparts. Often, two or more radioactive samples were fed to a single spider if an individual sample contained a comparatively low total amount of isotope. Spiders were not fed after ingestion of radioisotope but were given water daily. All subsequent webs built during the remainder of the experimental spiders' lives were collected for analysis. Note that spiders fed labeled whole orb web or major ampullate silk are referred to as web-fed and silk-fed spiders, respectively.

In addition to major ampullate silk, the ability of *A. cavaticus* to digest pulled minor ampullate silk was also examined, though to a much lesser extent since, in our experience, minor ampullate fibers cannot be pulled for long periods of time, as major ampullate fibers can. Also, the small amounts of minor ampullate silk obtainable made radiolabeling and partitioning of the silk impractical. Instead, digestion was only evaluated by observation of pinioned spiders under the dissecting microscope and by comparison of dry silk weights before and after feeding.

Some of the webs constructed by spiders fed radioactive material were collected intact on 20.3 cm x 25.4 cm glass plates and placed with Kodak™ SB-5 X-ray film as described previously (Kavanagh and Tillinghast 1979). The remainder of the webs were collected on micropipettes, hydrolyzed, and specific activities determined as described above. In addition, two dimensional thin layer chromatography (2D-TLC) was performed on some of the hydrolysates. Typically, 125 μ g leucine equivalent amounts were chromatographed, but occasionally the amount of hydrolysate remaining after specific activity determination necessitated the use of a lesser quantity. For 2D-TLC, 20 x 20 cm Merck® precoated cellulose plates, 0.1 mm thickness, were developed using the solvent systems of Schmidt (1974); pyridine:acetone:ammonium hydroxide:water (45:30:5:20, v/v) for the first dimension and 2-propanol:formic acid (88%):water (75:12.5:12.5, v/v) for the second dimension. Development from the sample origin was 16 cm in both dimensions. Autoradiograms were prepared from the TLC plates as for plated webs, following which amines were visualized using a 11mM ninhydrin in acetone solution.

In August and September the building of orb webs, particularly by gravid female *A. cavaticus*, becomes less reliable, at least in the laboratory, than earlier in the season. Typically, these spiders instead lay down a plentiful amount of "random" fibers throughout the cage, which are presumably of major ampullate gland and, secondarily, minor ampullate gland origin, predominantly. Certainly, it seems very unlikely that any aggregate gland material is used in these constructions. Accumulations of "random" fibers produced over one or more days, as well as any orbs built by such silk-fed and web-fed spiders, were collected on micropipettes and treated the same as described above for orb webs.

RESULTS

Following the digestion of web or silk by pinioned spiders, the remnant present between the endites, if any, was removed and used to estimate the percentage of

Table 1.—Solubilization of orb webs, major ampullate silk, and minor ampullate silk by pinioned *A. cavaticus*. The data from spiders fed whole orb webs have been separated into two groups to demonstrate the disparity between them (particularly with respect to the percentages determined by measuring radioactivity). Group 1 spiders were fed web on or between June 23 and July 11 and between 2130 and 0645 hours. Group 2 spiders were fed web on or between July 18 and August 23 and between 1100 and 1630 hours. Ninhydrin positive compounds were assayed using leucine as the standard.

| Material Fed to Spiders | Percentage of Web or Silk Remaining After Feeding (Mean \pm SE; Median) | | | n |
|-------------------------|--|---|--|----|
| | Gravimetrically Determined | As Determined by Measuring Ninhydrin Positive Compounds in Hydrolysates | As Determined by Measuring Radioactivity in Hydrolysates | |
| Orb Web Group 1 | 1.6 \pm 0.5; 1.6 | 2.9 \pm 1.0; 2.1 | 0.18 \pm 0.08; 0.089 | 5 |
| Orb Web Group 2 | 3.8 \pm 0.6; 3.9 | 2.9 \pm 0.7; 2.6 | 2.9 \pm 0.7; 2.9 | 4 |
| Maj Amp Silk Only | 1.0 \pm 0.4; 0.39 | 0.61 \pm 0.22; 0.35 | 0.12 \pm 0.10; 0.00 | 13 |
| Min Amp Silk Only | 97 \pm 13; 97 | — | — | 2 |

material which was not solubilized (Table 1). Of the three types of measurement used to make this estimate, that of measuring residual radioactivity was probably the most accurate as it would not have been influenced by non-sample materials incorporated into the remnants; principally hairs loosened from the endites' scopulae. The higher percentages most often obtained with the other two methods support this belief. Consistent with earlier *in vitro* studies (Kavanagh and Tillinghast 1979) minor ampullate silk was found to be relatively resistant compared to major ampullate silk. Spiders fed minor ampullate silk were unable to solubilize a large majority of the samples despite digestion attempts which were typical of spiders fed major ampullate silk or whole web, both in terms of method used and time involved. The contribution of non-sample inclusions to the remnants was made apparent in one of the two minor ampullate silk feedings by the weight of the remnant exceeding that of the original sample. In the second feeding 16% of the sample, by weight, was solubilized. Again, this figure may be somewhat low due to non-sample contaminants. Additionally, the former silk sample was subsequently fed to six successive spiders, wrapped each time with a new orb web to further encourage digestion. The remnant left by the sixth spider had a weight approximately three times that of the original sample, with contributions from the orb webs no doubt accounting for much of the increase in weight. Nevertheless, the original sample, which was whiter than the rest of the remnant, could still be distinguished and was not noticeably diminished by the six spiders.

By contrast, in eight out of thirteen major ampullate silk feedings either no remnant was left at all or no significant radioactivity (< 3 SD from the mean background count) was detectable in the remnant. In all cases a very large fraction of the sample was solubilized.

Unexpectedly, radioactivity measurements made on remnants from orb web feedings indicated two significantly different groups (approximate *t*-test, Sokal and Rohlf 1981; $P < 0.05$; Table 1). An examination of the feeding conditions for each of the spiders in these two groups revealed two consistent differences; the time of day and year during which feeding took place. Group 1 spiders were fed web on or between June 23 and July 11 and between 2130 and 0645 hours.

Table 2.—Efficiency in recycling ingested ^{14}C -labeled web and major ampullate silk components. Range and mean values reflect the total isotope present in all webs and/or "random" fibers collected from a given spider subsequent to feeding, expressed as a percentage of the total amount of isotope present in the material fed to the spider.

| Radioactive Material Fed to Spiders | Material Collected and Analyzed | ^{14}C -Radioactivity Recycled | | | n |
|-------------------------------------|---------------------------------|---|----------|--------|----|
| | | Range (%) | Mean (%) | SE (%) | |
| Orb Web | Orb Webs | 4.00-32.0 | 16.3 | 2.93 | 12 |
| Orb Web | Random Fibers, Orb Webs | 4.20-6.09 | 5.1 | 0.95 | 2 |
| Major Ampullate Silk | Orb Webs | 0.430-23.2 | 10.8 | 4.86 | 4 |
| Major Ampullate Silk | Random Fibers, Orb Webs | 2.91-23.7 | 13.2 | 1.85 | 12 |
| Total | | 0.430-32.0 | 13.6 | 1.57 | 30 |

Group 2 spiders were fed web on or between July 18 and August 23 and between 1100 and 1630 hours. Whether either or both of these differences were involved in producing the different solubilization percentages is unknown. Features common to both groups include a high percentage of solubilization, although, on average, not as high as for major ampullate silk, and incomplete solubilization in all cases (radioactivity in remnants > 5 SD from the mean background count).

The efficiency with which *A. cavaticus* was found to recycle ingested whole web or major ampullate silk is presented in Table 2. Total isotope present in all webs and/or "random" fibers produced by each spider after being fed radioactive material are expressed as a percentage of the total isotope present in the radioactive material fed. Considerable variability in this percentage was apparent, irrespective of the method used to feed the spiders. In no instance, however, did our recycling percentages even approach those determined by Peakall (1971) for *Araneus diadematus* Cl. Whereas we obtained a maximum recycling of 32%, which takes into account the total amount of isotope present in all webs constructed by the spider, Peakall (1971) typically found the percentage of recycled material in the first web constructed to be in excess of 90%. Earlier estimates of recycling for *A. diadematus* made by Breed et al. (1964) were more in keeping with our results, ranging from 21 to 50%. Their estimates were made from the total radioactivity present in the first two webs constructed by each spider.

The normalized specific activities of webs built by twelve spiders fed radioactive whole web and by four spiders fed radioactive major ampullate silk are presented in Figs. 1 and 2, respectively. Actual peak specific activities ranged from 2.0 to 47 CPM/ μg leucine equivalents in Fig. 1 and from 1.2 to 79 CPM/ μg leucine equivalents in Fig. 2. Taking into consideration the amount of isotope contained in the material fed, peak specific activities ranged from 9.8×10^{-6} to 3.3×10^{-4} CPM/(CPM in web fed $\times \mu\text{g}$ Leu equiv.) in Fig. 1 and from 1.9×10^{-5} to 2.7×10^{-4} CPM/(CPM in silk fed $\times \mu\text{g}$ Leu equiv.) in Fig. 2. For eleven of the twelve web-fed spiders, peak specific activity was present in the first web constructed, while all four silk-fed spiders attained peak specific activity in the second web built. 2D-TLC and subsequent autoradiography of hydrolysates prepared from these webs would indicate that GABamide (4-aminobutyramide) played a major role in producing this difference. GABamide is present in the adhesive spirals of those Araneidae examined thus far (Fischer and Brander 1960; Anderson and Tillinghast 1980; Tillinghast and Christenson 1984). Particularly strong support

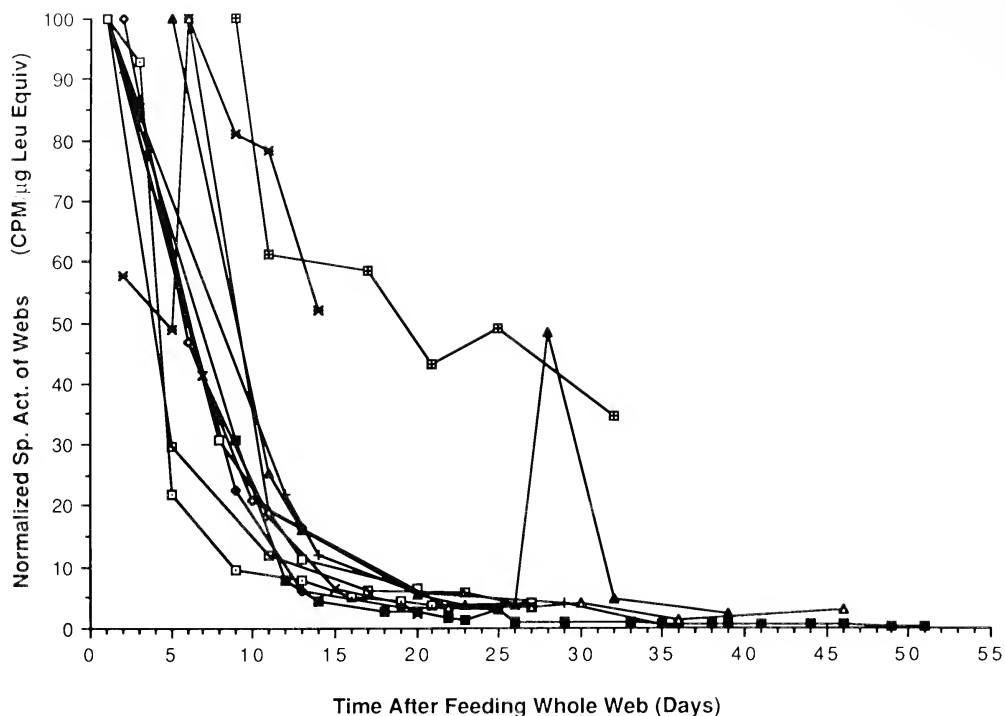


Fig. 1.—Incorporation of isotope into webs built by twelve spiders fed ^{14}C -labeled whole orb webs. The surge in specific activity at web 7 (day 28) from the spider represented by solid triangles was due entirely to isotope incorporation into UC8, as revealed by autoradiography of the 2D-TLC plate prepared from this web's hydrolysate.

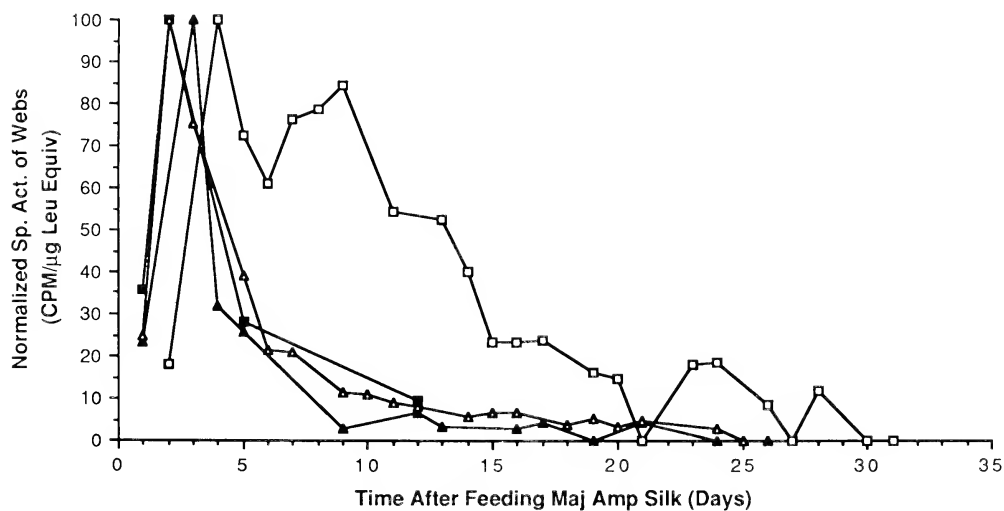


Fig. 2.—Incorporation of isotope into webs built by four spiders fed ^{14}C -labeled major ampullate silk.

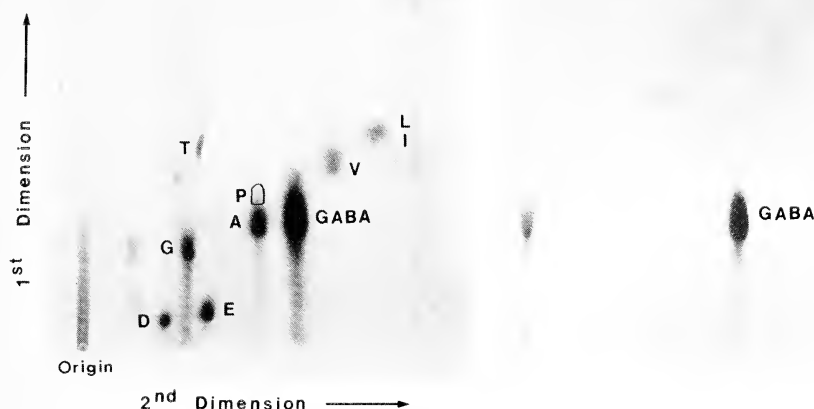


Fig. 3.—2D-TLC of three pooled web 1 hydrolysates from web-fed spiders. Of the 125 μg leucine equivalents chromatographed, 34 μg were from a web with a sp. act. of 47 CPM/ μg Leu equiv. (built 1 day after feeding, represented in Fig. 1 by a solid diamond), 77 μg were from a web with a sp. act. of 30 CPM/ μg Leu equiv. (built 1 day after feeding, represented in Fig. 1 by an open square), and the remaining 14 μg were from a web with a sp. act. of 43 CPM/ μg Leu equiv. (built 2 days after feeding, represented in Fig. 1 by an open diamond). An exposure of 110 days was used to produce the autoradiogram (right). A = alanine; D = aspartic acid; E = glutamic acid; G = glycine; GABA = 4-aminobutyric acid; I = isoleucine; L = leucine; P = proline; T = threonine; V = valine. Proline has been circled in the chromatogram since a yellow product, difficult to see in black and white photographs, is formed when proline is reacted with ninhydrin.

for this proposal came from the first webs built by three of the web-fed spiders, two of which were built 1 day after feeding and one which was built 2 days after feeding. In these webs' hydrolysates virtually all of the isotope was restricted to GABA (4-aminobutyric acid; Fig. 3), the hydrolytic product of GABamide. Less extreme results were obtained from the other hydrolysates chromatographed (Figs. 4, 5, 6). For the spider whose webs are presented in Fig. 4, GABamide was still the major radioactive compound present in the first web built after feeding, but some amino acids and as yet unidentified compounds were also carrying label. Note that web 1 was built 5 days after feeding. In Fig. 5, GABA and an unidentified compound (UC1) can be seen to possess comparable amounts of isotope in web 1, with other unidentified compounds containing considerably lesser amounts. Web 1 of Fig. 6, built 6 days after feeding, again shows GABA dominating the autoradiogram. Thus, despite the concurrent high specific activity of UC1 in one instance, it was GABamide which appeared to be responsible for the maximum specific activities most often occurring at web 1 in web-fed spiders. The single exceptional web-fed spider produced atypical webs having few or no adhesive spiral loops. In the chromatogram prepared from this spider's first web GABA was only barely discernible and in chromatograms prepared from subsequent webs GABA was not visible at all.

In contrast, while GABA could clearly be seen in 2D-TLC autoradiograms prepared from the second webs built by silk-fed spiders, it certainly did not carry the majority of the label (Figs. 7, 8). Rather, several of the amino acids prevalent in web proteins were evidently responsible for the peak specific activities in the second webs of these spiders.

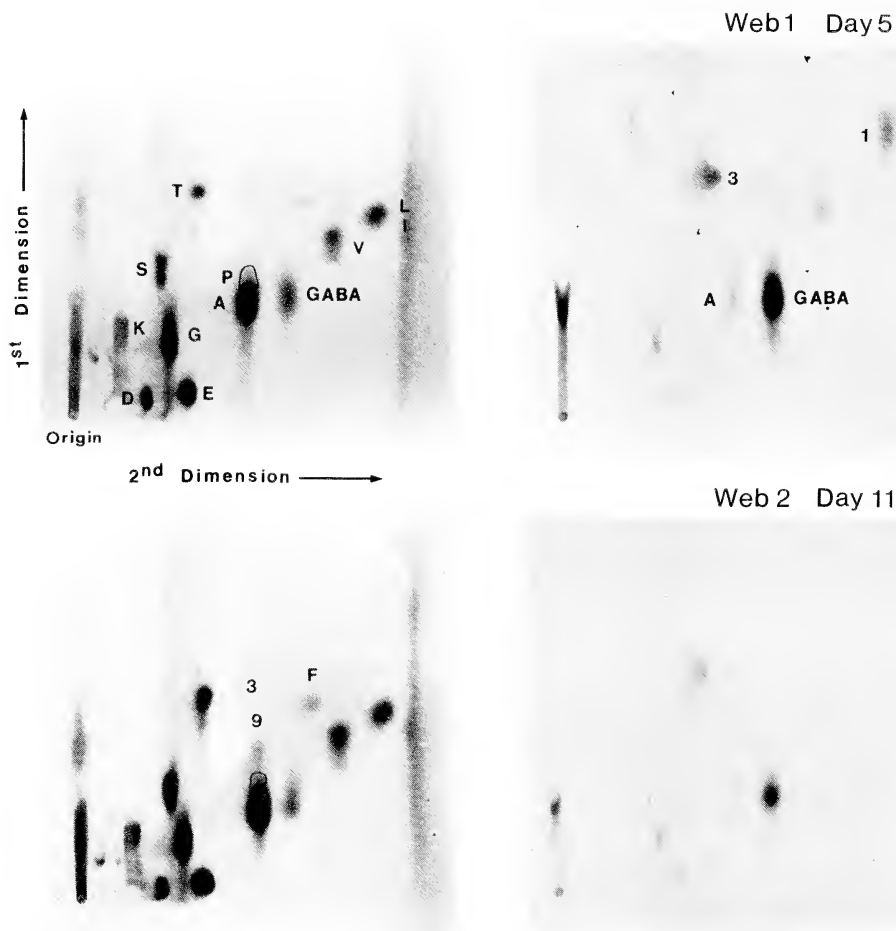


Fig. 4.—2D-TLC of hydrolysates (125 μ g Leu equiv.) made from the first two webs built by a web-fed spider. These webs are represented in Fig. 1 by solid triangles. Autoradiograms form the right side of each pair. Sp. act. (CPM/ μ g Leu equiv.): web 1, 14; web 2, 3.6. X-ray film exposures (days): web 1, 119; web 2, 122. A = alanine; D = aspartic acid; E = glutamic acid; F = phenylalanine; G = glycine; GABA = 4-aminobutyric acid; I = isoleucine; K = lysine; L = leucine; P = proline; S = serine; T = threonine; V = valine. Numbers designate unidentified compounds (UC).

Autoradiograms prepared from plated webs were consistent with the TLC results. Thus, the first webs built by three web-fed spiders had adhesive spirals which were much more intensely labeled than radii or hub spirals. The adhesive coverings were particularly dark, especially considering the extent to which they were smeared during preparation for autoradiography. Subsequent webs had less intense adhesive coverings and were apparently less labeled overall. In the second webs built by two silk-fed spiders, the radii and adhesive spirals were of roughly equal intensity and the adhesive spiral core fibers appeared to contain the majority of the adhesive spirals' isotope. Peak activity was apparently possessed by these second webs.

Also instructive were the results obtained when collections of "random" fibers, in addition to any webs constructed, were analyzed. The normalized specific activities of such collections and webs, produced by two web-fed spiders, are presented in Fig. 9. Likewise, those produced by ten silk-fed spiders are shown in

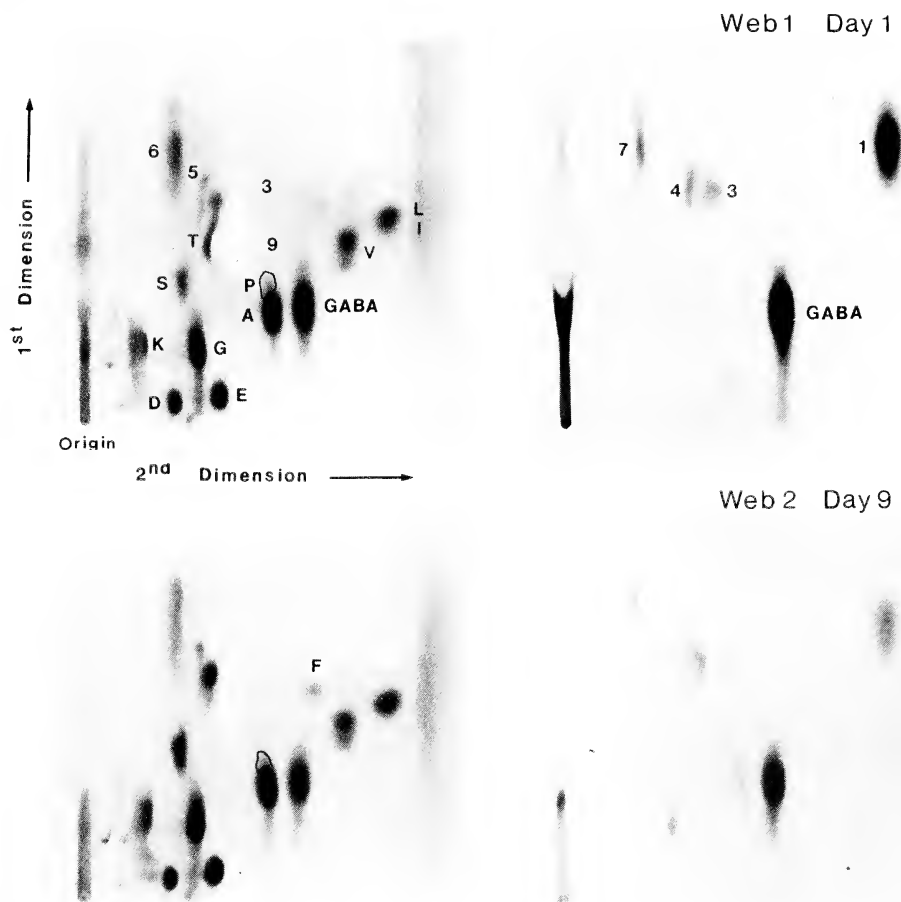


Fig. 5.—2D-TLC of hydrolysates (125 μ g Leu equiv.) made from the first two webs built by a web-fed spider. These webs are represented in Fig. 1 by solid squares. An exposure of 111 days was used to produce the autoradiograms (right side of each pair). Sp. act. (CPM/ μ g Leu equiv.): web 1, 38; web 2, 12. See Fig. 4 for explanation of symbols.

Fig. 10. Unlike the trend observed in Fig. 1, the maximum specific activity was not present in the first collection of “random” fibers from either of the web-fed spiders (Fig. 9). Assuming the construction of “random” fibers does not involve aggregate gland secretions, it would seem that this difference was due to the lack of an outlet for ingested radioactive GABamide as GABamide. Note that one of the web-fed spiders built nine webs following the collection of the first “random” fibers and that the first web built possessed the highest specific activity. 2D-TLC and autoradiography of this first web revealed that while radioisotope was clearly present in glycine, alanine, glutamic acid, aspartic acid, and serine, GABA and two unidentified compounds (UC2, UC3) contained the majority of the isotope (Fig. 11). GABA’s intensity on the autoradiogram was particularly striking considering the relatively low amount of GABA demonstrated by the chromatogram. Apparently, with the building of the first web, an outlet for GABamide was provided, resulting in peak activity. Actual peak specific activities in Figure 9 were 0.28 CPM/ μ g leucine equivalents [3.8×10^{-6} CPM/(CPM in

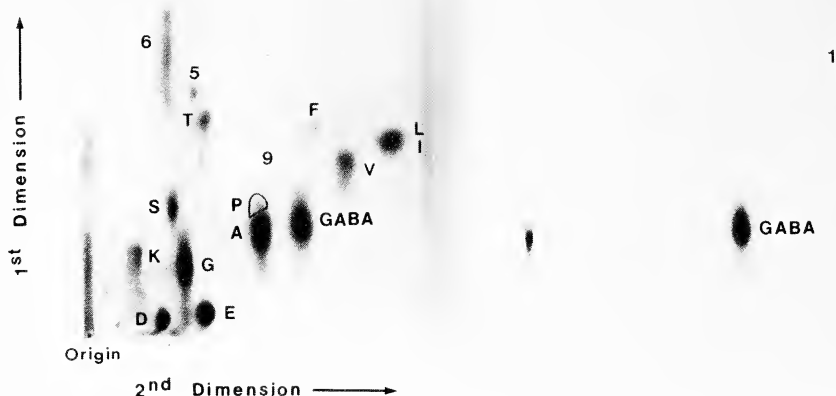


Fig. 6.—2D-TLC of a web 1 hydrolysate (125 μg Leu equiv.) from a web-fed spider. The web, built 6 days after feeding and having a sp. act. of 11 CPM/ μg Leu equiv., is represented in Fig. 1 by an open triangle. An exposure of 119 days was used to produce the autoradiogram (right). See Fig. 4 for explanation of symbols.

web fed $\times \mu\text{g}$ Leu equiv.)] for the spider from which only “random” fibers were collected and 12 CPM/ μg leucine equivalents [5.2×10^{-5} CPM/(CPM in web fed $\times \mu\text{g}$ Leu equiv.)].

Of the ten silk-fed spiders (Fig. 10), peak activity was present in the first collections of “random” fibers produced by three of these spiders, in the second collections produced by six of the spiders, and in the third collection produced by the tenth spider. Recalling that peak activity in second webs built by spiders fed major ampullate silk was apparently due to several common web protein residues (Figs. 7, 8), it is not surprising that peak activity for the majority of the spiders in Fig. 10 occurred in the second or third “random” fiber collections. Such protein residues are obviously utilized in “random” fibers as well as in webs. The occurrence of peak activity in first and third collections may simply reflect the variability inherent in the time between the synthesis of progenitive silk components and their inclusion in drawn silk fibers. Alternatively, while it was our intent to obtain comparable amounts of “random” fibers during each collection, we found that similar appearing fiber accumulations in the cages sometimes possessed deceptively and considerably different weights. Most probably, both of these sources of variability contributed to the observed results. In contrast to the single case in Fig. 9, no silk-fed spider produced a web with a specific activity significantly higher than the “random” fibers produced just prior to it, indicating that ingested radioactive GABamide was the source of most of the radioactive GABamide seen in the first web of Fig. 9. Actual peak activities in Fig. 10 ranged from 0.077 to 15 CPM/ μg leucine equivalents [3.2×10^{-6} to 3.4×10^{-5} CPM/(CPM in silk fed $\times \mu\text{g}$ Leu equiv.)]

DISCUSSION

It is clear from the web feeding trials that *A. cavaticus* is able to solubilize the vast majority of the orb web, a fact which was not revealed by the *in vitro* studies

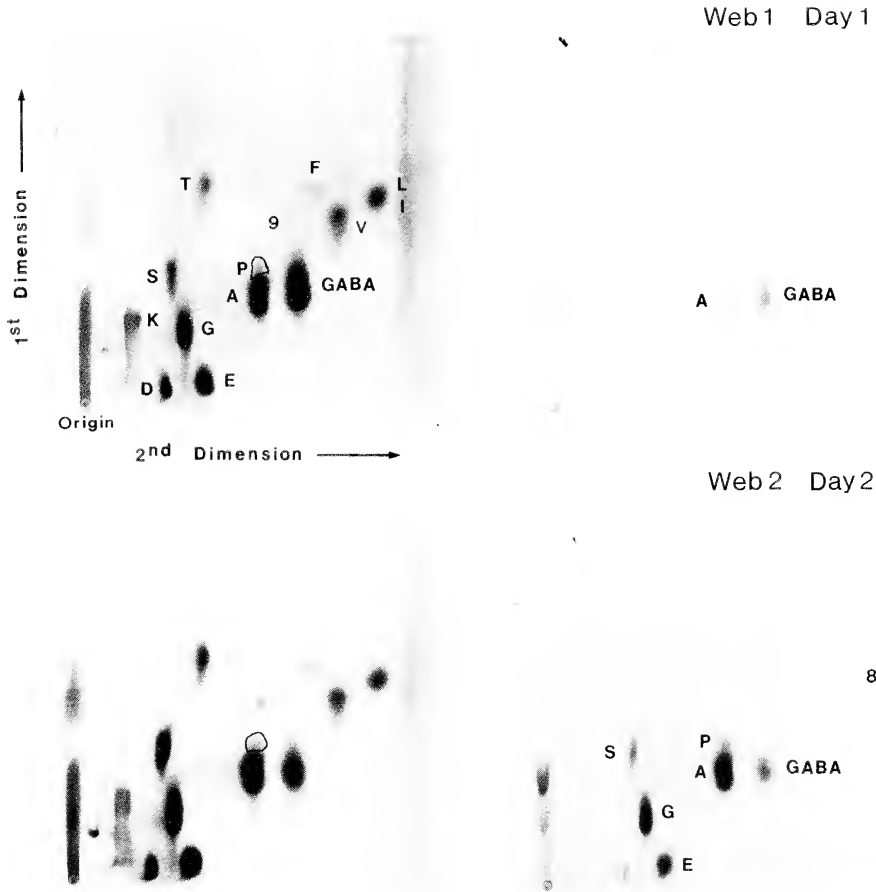


Fig. 7.—2D-TLC of hydrolysates made from the first two webs built by a silk-fed spider. The amounts chromatographed were 125 μ g Leu equiv. from web 1 and 140 μ g Leu equiv. from web 2. These webs are represented in Fig. 2 by open triangles. An exposure of 111 days was used to produce the autoradiograms (right side of each pair). Sp. act. (CPM/ μ g Leu equiv.): web 1, 3.1; web 2, 12. See Fig. 4 for explanation of symbols.

on rod-wound web (Tillinghast and Kavanagh 1977). Not only was a greater percentage of the web solubilized *in vivo*, but at a clearly greater rate, such that more digestion occurred *in vivo* within 20 min than occurred *in vitro* within 24 h. Certainly these differences must have been in part a result of the digestive fluid dilution made during the *in vitro* studies; a factor which may have been important not just because of the lowered protease concentration. As proposed earlier (Kavanagh and Tillinghast 1983), digestion may also require or be facilitated by non-enzymatic components in the digestive fluid, such as surfactants, which would also have been diluted. In addition, observations on pinioned spiders indicate that the contribution of mastication and digestive fluid replenishing to orb web digestion is considerable. Spiders frequently rotated, pierced, and compressed web or silk samples using their fangs and endites, and, often at very short intervals, ingested the digestive fluid already surrounding a sample, only to regurgitate more digestive fluid immediately thereafter. These

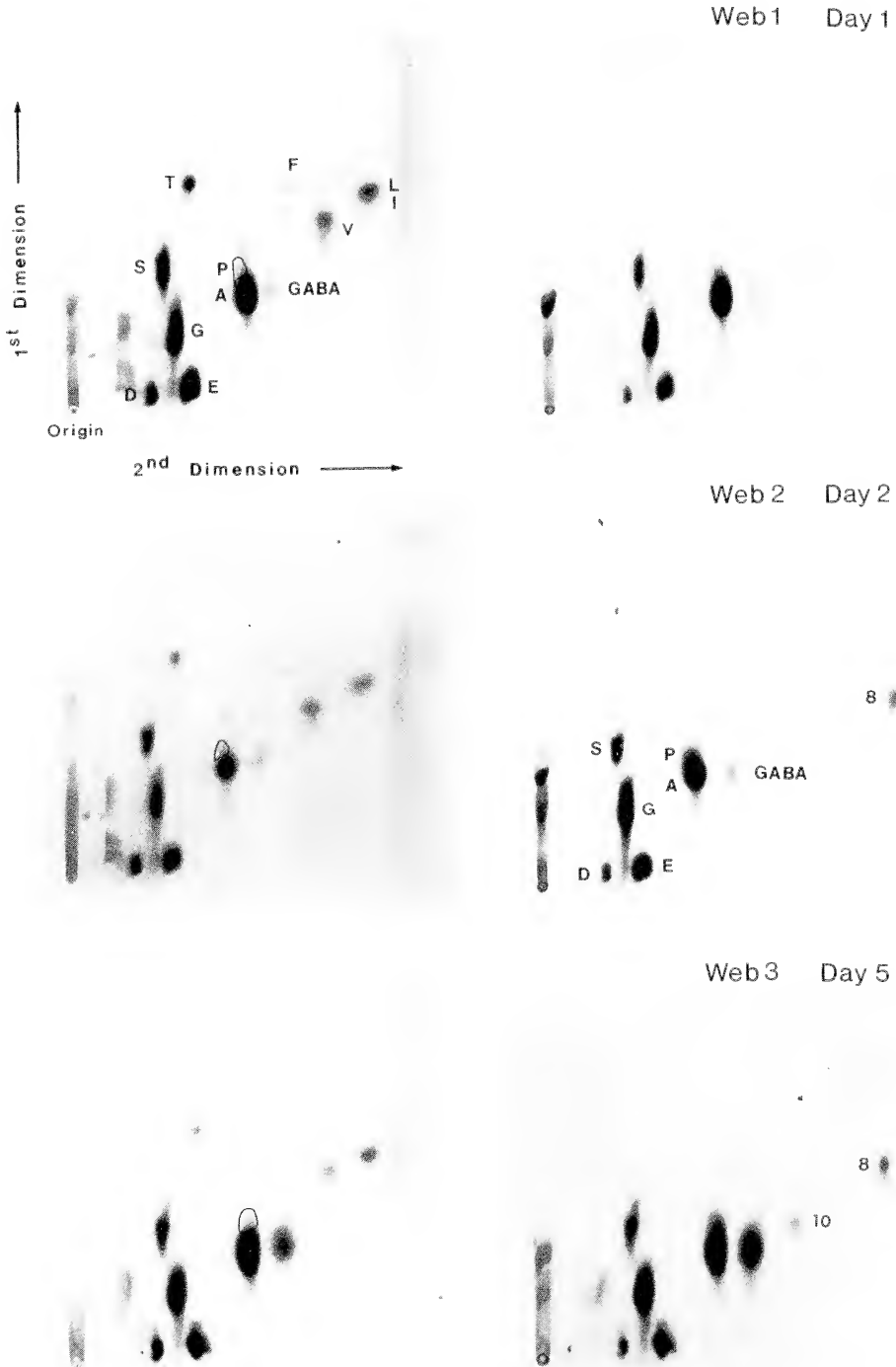


Fig. 8.—2D-TLC of hydrolysates made from the first three webs built by a silk-fed spider. The amounts chromatographed were 125 μ g Leu equiv. from webs 1 and 3, and 60 μ g Leu equiv. from web 2. These webs are represented in Fig. 2 by solid squares. An exposure of 122 days was used to produce the autoradiograms (right side of each pair). Sp. act. (CPM/ μ g Leu equiv.): web 1, 28; web 2, 79; web 3, 22. See Fig. 4 for explanation of symbols.

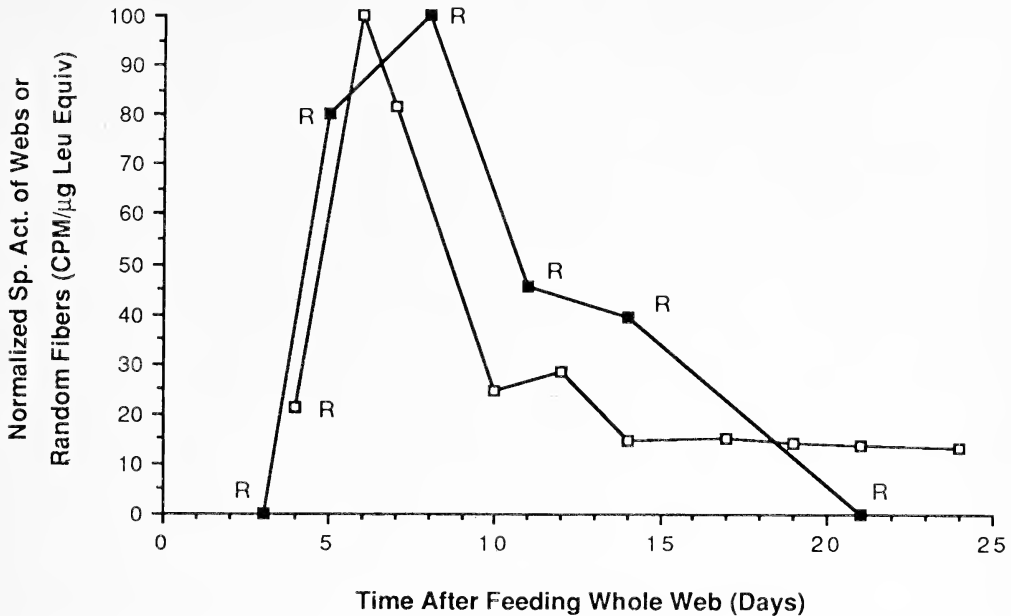


Fig. 9.—Incorporation of isotope into webs and “random” fibers produced by two spiders fed ^{14}C -labeled whole orb webs. R = collections of “random” fibers.

actions presumably helped to hasten and maintain exposure of the entire sample to active enzyme.

Despite the greater extent of orb web solubilization *in vivo*, complete solubilization was still never achieved. Unlike the situation *in vitro*, however, the small percentage of nonsolubilized web which remained *in vivo* does not preclude the possibility that the remnants were composed primarily of minor ampullate silk. In fact, the percentage of web remaining after some feedings was so small as to indicate that minor ampullate silk must be at least partially digestible. The possibility that these webs may simply have contained very few or no minor ampullate fibers cannot be excluded, but seems unlikely based on observations of minor ampullate fiber occurrence in orb webs (Kavanagh and Tillinghast 1979; Work 1981). Moreover, evidence for partial digestion was also obtained in one of the two minor ampullate silk feedings. Kovoov (1972) has demonstrated the composite nature of minor ampullate fibers from *A. diadematus* through a comparison of the distal and proximal minor ampullate cell types. The granules secreted into the lumen by these two cell types were found to be histochemically distinct. This raises the possibility that partial digestion could result from the selective digestion of one or more of the component species of minor ampullate fibers.

At present we cannot explain the large discrepancy between the recycling efficiencies we obtained and those of Peakall (1971). A number of differences in the materials and methods used could have contributed to this discrepancy. These differences included the species of *Araneus* used, the radiolabeled compound fed, and the method used to estimate the total amount of isotope in the ingested web. Also, Peakall considered the time between web recycling and new web construction to be critical to efficient recycling; a time which in *A. diadematus* was reportedly not more than one hour. As a consequence of the methods we

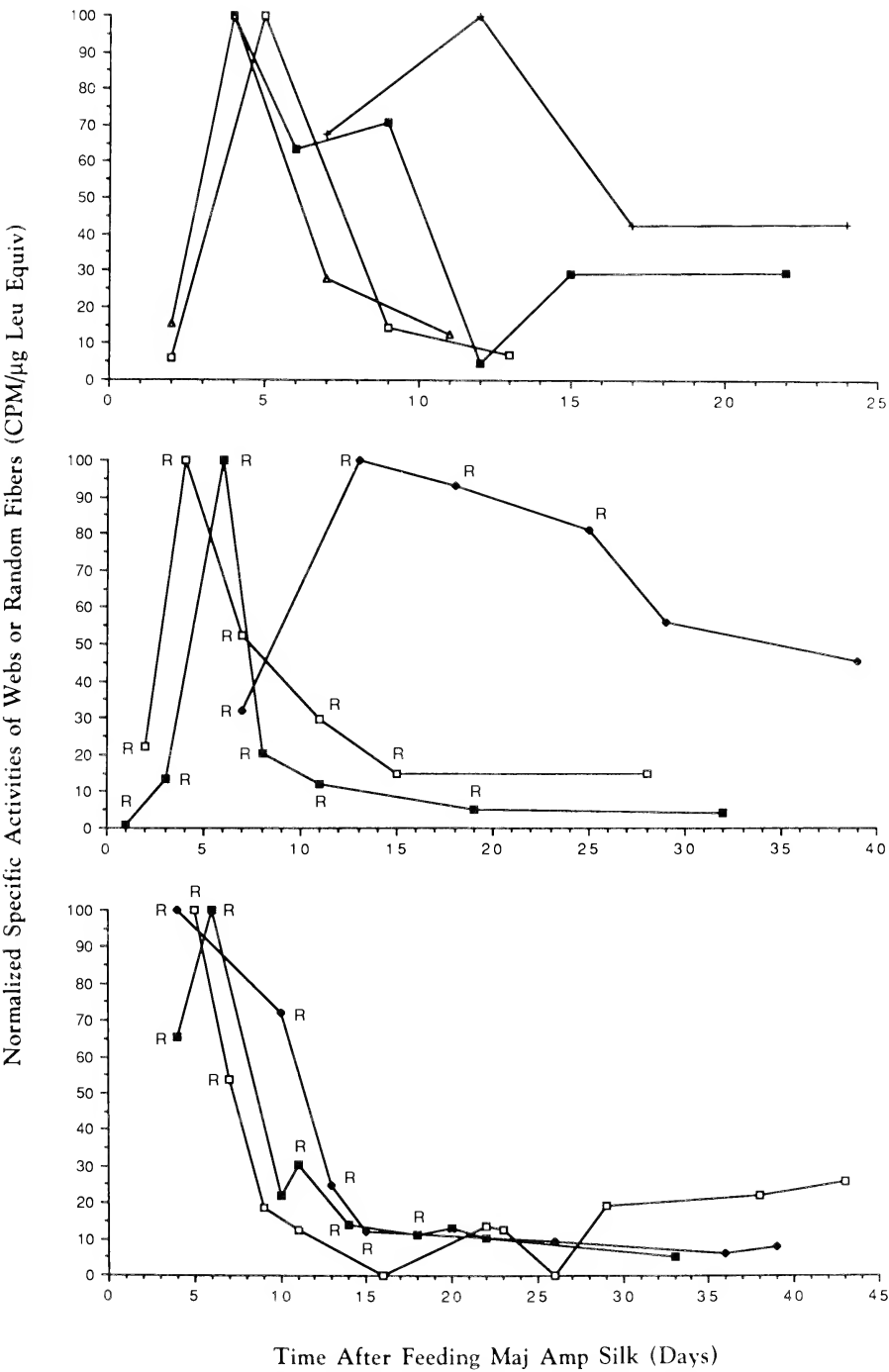


Fig. 10.—Incorporation of isotope into webs and “random” fibers produced by ten spiders fed ^{14}C -labeled major ampullate silk. All data points in the top graph were obtained from “random” fiber collections. In the center and bottom graphs, an R designates “random” fiber collections. The ten spiders were separated into three graphs merely for the sake of clarity. Note the different ranges of the abscissas.

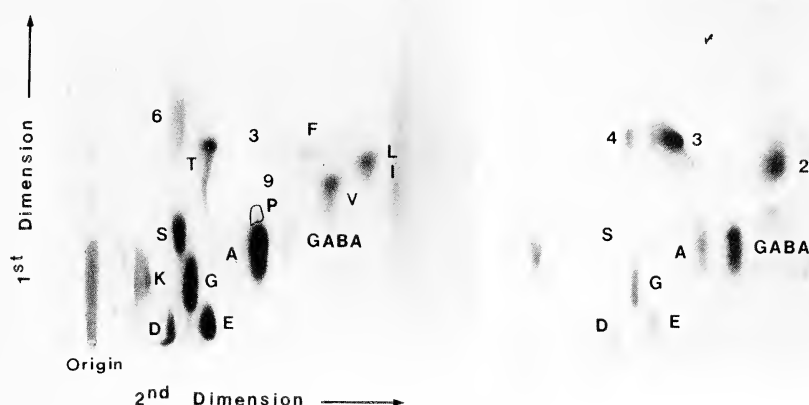


Fig. 11.—2D-TLC of a web 1 hydrolysate (125 μg Leu equiv.) from a web-fed spider. The web, built 6 days after feeding and after one “random” fiber collection was made, is represented in Fig. 9 by an open square. Sp. act. 12 CPM/ μg Leu equiv. An exposure of 117 days was used to produce the autoradiogram (right). See Fig. 4 for explanation of symbols.

used to feed web, this interval was either over ten hours or under ten hours but unknown in our experiments on recycling efficiency. Thus, additional experiments in which this interval is shortened will be required to better evaluate Peakall's claim. Solely on the basis of the digestibility of the orb web as determined *in vivo*, and contrary to the previous *in vitro* findings, the high recycling efficiency reported by Peakall is at least plausible.

From the specific activities of the successive webs built by spiders fed radioactive web or silk, along with the chromatograms and autoradiograms prepared from those webs' hydrolysates, it would appear that on average ingested GABamide is reutilized in new web more quickly than ingested protein residues. Thus, the first web constructed by a spider fed whole web usually had a higher specific activity and more total isotope than webs produced subsequently, and the relatively high specific activity of GABamide in the first web was apparently responsible for this trend. In contrast, for spiders fed major ampullate silk, peak activity and the largest total amount of isotope were present in the second webs constructed, and protein residues, particularly alanine, glycine, glutamic acid, and serine, possessed a large majority of the isotope in these webs. The results from web-fed spiders which produced constructions lacking GABamide (i.e., “random” fibers; Fig. 9) were more similar to those from silk-fed spiders and lend further support for GABamide's more rapid reutilization. As radiolabeled GABamide was present in the webs of spiders fed major ampullate silk (Figs. 7, 8), it is reasonable to assume that non-GABamide web components were also used to synthesize some of the labeled GABamide present in webs built by web-fed spiders. However, since GABamide was responsible for peak specific activity only in webs built by web-fed spiders, it is also reasonable to assume that most of the radioactive GABamide in these webs must have come from radioactive GABamide in the ingested web.

The results also indicate that a sizable fraction of the ingested GABamide may remain available for incorporation into new web for at least several days, should web construction be forgone for such a period. Whether this is due to an actual

sequestration of GABamide or a resistance to metabolic conversion or both cannot be stated. Whatever the cause, it was found that the first web built by a web-fed spider could still, as a result of GABamide, have peak specific activity and the largest total amount of isotope even if 5 (Fig. 4) or 6 (Fig. 6) days elapsed between feeding and its construction. Somewhat similar results were obtained from another web-fed spider despite a substantial quantity (1.16 mg Leu equiv.) of "random" fibers being laid down before web 1's construction; which was 6 days after feeding (Fig. 11). However, in this instance GABamide, UC2, and UC3 were each influential in producing the maximum specific activity. Again, that the majority of GABamide's label in these three webs was from ingested GABamide is indicated by the results from silk-fed spiders; in particular, the observation that isotope in the web with the highest specific activity was not localized primarily in GABamide.

Due to the radiolabeled compound used, no data were obtained on other known components of the adhesive spiral's covering, such as the inorganics, KH_2PO_4 and KNO_3 (Schildknecht et al. 1972). This was also true for taurine, obtained by acid hydrolysis from the adhesive spiral's taurine derivative(s) (Fischer and Brander 1960; Anderson and Tillinghast 1980), since ^{14}C -labeling of this compound was meager at best in spiders fed radiolabeled web or silk. Thus, it is not known if GABamide's behavior is shared by other low molecular weight adhesive spiral components.

During the course of the 2D-TLC, several unidentified compounds have repeatedly been encountered and designated UC1-UC10 (Figs. 3-8, 11). UC1-UC4, UC7, UC8, and UC10 are ninhydrin negative but can incorporate isotope when spiders are fed ^{14}C -glucose. UC5 and UC6 are ninhydrin positive but have not been found to incorporate isotope. UC9 is neither ninhydrin positive nor does it become radioisotopically labeled by ^{14}C -glucose. However, the cellulose support of the TLC plates fortuitously takes on a light purple background hue with ninhydrin visualization, which UC9 inhibits. Thus, within about 1 day after application of the ninhydrin spray, UC9 makes its presence known by the white spot it leaves on the chromatogram. UC3 behaves similarly to UC9 in this respect.

ACKNOWLEDGMENTS

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SEXUAL BEHAVIOR IN *DICTYNA VOLUCRIPES* (ARANEAE, DICTYNIDAE)¹

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ABSTRACT

Courtship and mating in *Dictyna volucripes* Keys. are described on the basis of laboratory observations of 13 virgin pairs. Their behavior conformed well to the general pattern within the family. Various features of both female and male behavior are consistent with the view that courtship functions mainly in influencing mate-choice by females, rather than in inhibiting predatory attack upon males.

Laboratory and field observations show that pairs commonly remain together for some days after mating. While the function of such cohabitation is unknown, it can evidently provide an important preadaptation in the evolution of spider sociality.

INTRODUCTION

The Dictynidae is a widespread family of small to medium-sized, cribellate spiders which make irregular webs. In recent years much attention has focused on the permanently social *Mallos gregalis* (Simon), which has in turn called comparative attention to the behavior of more typically solitary or intermediate species (Honjo 1977; Jackson 1977-1979; Uetz 1983).

Observations of courtship and mating have been reported from about 12 species of Dictynidae (Karpinski 1882; Montgomery 1903; Berland 1916; Gerhardt 1924; Locket 1926; Billaudelle 1957; Leech 1966; Bristowe 1971; Jackson 1979). Before Jackson's (1979) analysis of sexual behavior in two *Mallos* species and *Dictyna calcarata* Banks, observation was mostly rather superficial, with few quantitative data. As a result, comparisons based on the older literature are often inconclusive.

Jackson (1979) has reviewed sexual behavior in the family. In this paper I describe courtship and mating in an additional species, with some remarks on post-mating cohabitation.

Dictyna volucripes Keys. is widespread in eastern North America (Chamberlin and Gertsch 1958) and often locally abundant. In eastern Kansas I have found the web typically in the upper part of a small plant, where it forms an irregular tent over a flowerhead or several twigs. A small region of the interior is

¹Contribution no. 1974 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045. This paper is dedicated to Willis J. Gertsch on the occasion of his 80th birthday, 4 October 1986. Dr. Gertsch has been very generous to me and many other amateur arachnologists.

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Fig. 1.—Part of a *D. volucripes* web with a mating pair in the retreat area. The opening to the retreat is in the middle foreground.

reinforced with silk to form a distinct, tubular retreat (Fig. 1). The spider is most often found motionless within the retreat. For a clear illustration of web structure in a related species, see Bristowe (1971: Fig. 41).

Preliminary observations in old fields in eastern Kansas indicate that *D. volucripes* usually overwinters in the subadult stage and that males molt to adulthood a few days before females. Sexual dimorphism is not pronounced, with adult females only slightly larger than males. Scheffer (1905) reported the appearance of egg-sacs in the webs from late June to late September in this area, with 15 eggs/sac and usually 1-5 sacs/web.

MATERIALS AND METHODS

Female and male subadult spiders were collected in northeastern Kansas in March-April of 1975 and 1976. Individuals were reared to adulthood in separate vials, so that all were known to be virgin when first paired. Both as subadults and adults, spiders were provided with flies (*Drosophila* sp.) as prey and appeared well fed, except as otherwise noted. Newly emerged females were introduced onto separate dry, tree-like plant stalks (henceforth called "trees") which simulated wild web-sites and then left to spin webs. Each tree was held upright in sand and covered with a large glass jar, so that it was free on all sides. After 1-3 days, the jar was removed, an adult male introduced at the tree base, and behavior noted with the aid of a tape recorder and hand lens. After a pair had shown no apparent sexual behavior for at least 30 min, we ended observation and replaced the jar. The pair was checked daily for the next four days for a general indication of its condition.

Specimens from Kansas collected and determined by C. K. Starr in 1975-1976 can serve as vouchers. These are deposited in the Snow Entomological Museum at the University of Kansas and the Canadian National Collection in Ottawa.

RESULTS

The following account is based on observation of 13 pairs. In three of these the female had been kept without food for up to two weeks; in all others both partners were well fed. An additional pair which showed no apparent pattern of sexual behavior is disregarded.

Courtship.—At the time of male introduction, the female was usually in the retreat in the **at-rest** posture (Fig. 4): motionless, body lying against the substrate and the legs drawn in close. The male usually began immediately to climb the tree and always reacted strongly upon touching the female's silk. Typically, he walked extensively on the outside of the web, laying down silk. Such **ranging-spinning** was usually rapid and often had a notably agitated appearance. The abdomen twitched up and down, and the pace of walking was very uneven. The palps were held in front, alternately lowered and raised.

The female's first reactions to ranging-spinning could in each case be interpreted as alertness to a potential prey or intruder. She came out of at-rest, extending her legs and raising her body off the substrate. Often she walked out of the retreat, and in some cases rushed toward the male, though without coming very close. As ranging-spinning proceeded, the female showed less and less reaction, and in most cases she entered the retreat and returned to at-rest within a very few minutes.

After several minutes, ranging-spinning gave way to a new phase, **local-spinning**, in which the male walked much more closely around the female and sometimes came to walk directly upon her. In two trials the female moved a short distance away from the male, but in others she remained still. Local-spinning evidently added silk to the retreat, as this came to appear denser. When the male walked upon the female, it appeared from movements of his abdomen that he bound her very lightly with silk.

During both ranging-spinning and local-spinning, males showed little response to female behavior. I could see no reaction when a female simply became alert inside the retreat or walked just outside it. The few times that a female rushed at the male, he retreated on the web, to remain briefly inactive before resuming ranging-spinning. In no case did the female chase a retreating male.

Two trials were performed with a male released at the base of a tree from which the female was newly removed, in order to see his reactions to the web alone. In each case, he went through ranging-spinning and local-spinning as if a female were present.

Local-spinning was followed by a phase in which the pair remained in direct physical contact. In all trials this began with the male coming face to face with the female, their faces apparently touching. This was followed by a period, usually lasting a few minutes, in which the male stroked the female's cephalothorax and parts of her legs with his palps, forelegs, second legs, and occasionally his third legs. As this proceeded, he appeared to attempt to raise her venter away from the substrate with his legs, and in trials which included mating



Fig. 2.—Mating pair of *D. volucripes*.

the **stroking-phase** ended with her rising up. In some trials, this phase was interrupted by a brief return to local-spinning, and in some the female broke contact and moved slightly away, in which case the male local-spun for a time before resuming face-to-face contact and stroking.

Female behavior in the stroking-phase, where she did not break contact, appeared almost entirely passive. She never stroked the male and at most drew her legs in still closer to the body.

Mating.—Raising of the female by the male was always quickly followed by a palpal insertion and was evidently a necessary prelude to it. In three trials without raising there was no insertion, even though in one of these the male courted for more than an hour. In 10 trials with insertion, courtship (comprising the ranging-spinning, local-spinning and stroking phases) lasted for 10-93 min, with a mean of 30 min. In five of nine trials the first insertion was with the left palp, while in four it was the right; in the 10th trial it was not noted.

The mating position in all cases was a variant of Gerhardt and Kaestner's (1937) position I (Figs. 2-3). The male's face was toward the female's sternum, so that the two bodies formed an approximately right angle. The male was rotated to one side, so that one palp was closer than the other to her epigynum, and this palp was inserted. The period of first continuous insertion was very variable, lasting 1-109 min (mean = 56 min, SD = 36 min).

During mating, the hematodocha of the palp pulsated rhythmically. Most of the time it was dilated, with very brief, strong contractions at intervals. In 15 insertions in which a sample of pulsations was timed, the mean interval between contractions was 6.7 s (range = 2-12 s, SD = 2.2 s), with most samples in the 7-9 s range. One male showed an unusual pattern of pulsations during two insertions: after a series of regular, brief contractions, the hematodocha remained contracted for several seconds before the next series of regular contractions.



Fig. 3.—Drawing based on Fig. 2. Female in white, male in black.

Further courtship and mating.—At the end of the first insertion phase, the pair disengaged simply and directly. Subsequent behavior was less predictable than that leading up to insertion. The observed variants can be divided into four groups:

- a. *No sexual activity.* In two trials the pair soon became motionless and remained so for the rest of the observation period. This was also the usual pattern following final insertion in the next two variants, the pair remaining at rest in or near the retreat (Fig. 4). One of the two pairs was noticed mating again the next day.
- b. *Courtship without mating.* In two trials the male resumed local-spinning for a short time, though without subsequent stroking. Courtship in these cases seemed weak and progressively disorganized.
- c. *Courtship with mating.* In three trials resumed courtship culminated in insertion of the other palp. In one of these, ranging-spinning preceded local-spinning and stroking. Respective durations of courtship were 12, 25 and 32 min. In the latter the female seemed resistant, as the male made several apparent attempts to raise her before he succeeded. In another of these trials the male again inserted the first palp almost immediately after his second withdrawal, without a return to courtship.
- d. *Mating without courtship.* In the remaining three trials the male inserted the second palp without a prior return to courtship. The intervening period was at most about 4 min. In one of these trials the spiders then remained at rest for 79 min, after which the male again inserted the first palp, and almost immediately upon withdrawing it he again inserted the second palp. Another trial was marked by extreme brevity in both insertions and apparent strong unreceptivity of the female after the second withdrawal. It was unclear which partner actively broke contact, but immediately after the first withdrawal the male briefly and unsuccessfully attempted to re-insert the same palp. After the second withdrawal he courted intermittently but vigorously for more than an hour, without further mating that day.

The eight recorded second and subsequent insertions had durations of 4-60 min (mean = 31 min, SD = 23 min). If we disregard the (apparently anomalous) one-minute first insertion, these eight later insertions are significantly shorter (*t*-test, $P < 0.05$).



Fig. 4.—*D. volucripes* pair at rest in web after mating. Female above, male below.

Cohabitation.—We made no systematic observations on the tendency of females and males to occupy webs together, but there are indications that they may commonly do this for extended periods. In the laboratory, pairs left undisturbed after mating remained without apparent conflict during the four days of observation, much of the time together in the retreat. Although the spiders were confined within the glass jar, either could have moved out of the tree and web. In the field later in the season I have often found an adult male in the web together with a female and her egg-cases.

It is also not rare to find more than two spiders in a web. A casual search of perhaps 30-40 occupied webs during two days in April 1976 showed six of them each with three spiders: four with a female and two males, two with two females and a male.

DISCUSSION

Comparison of sexual behavior in *Dictyna volucripes* with what is known from other dictynids shows this species to be quite generalized for the family. Its pattern of courtship and mating is especially close to that described by Billaudelle (1957) from *D. civica* (H. Luc.). Each of the behaviors recorded from *D. volucripes* appears to occur in at least one other species. Among the generalized features of *D. volucripes* sexual behavior are: twitching of the male's abdomen during spinning, face-to-face approach and stroking, mating position I, insertion of one palp at a time, alternation of palps in subsequent insertions, tendency to remain together for some days after mating, and the overall lack of aggression within the pair. I have assumed that abdominal twitching and face-to-face contact are each homologous in different species, though Jackson (1979) noted differences in form.

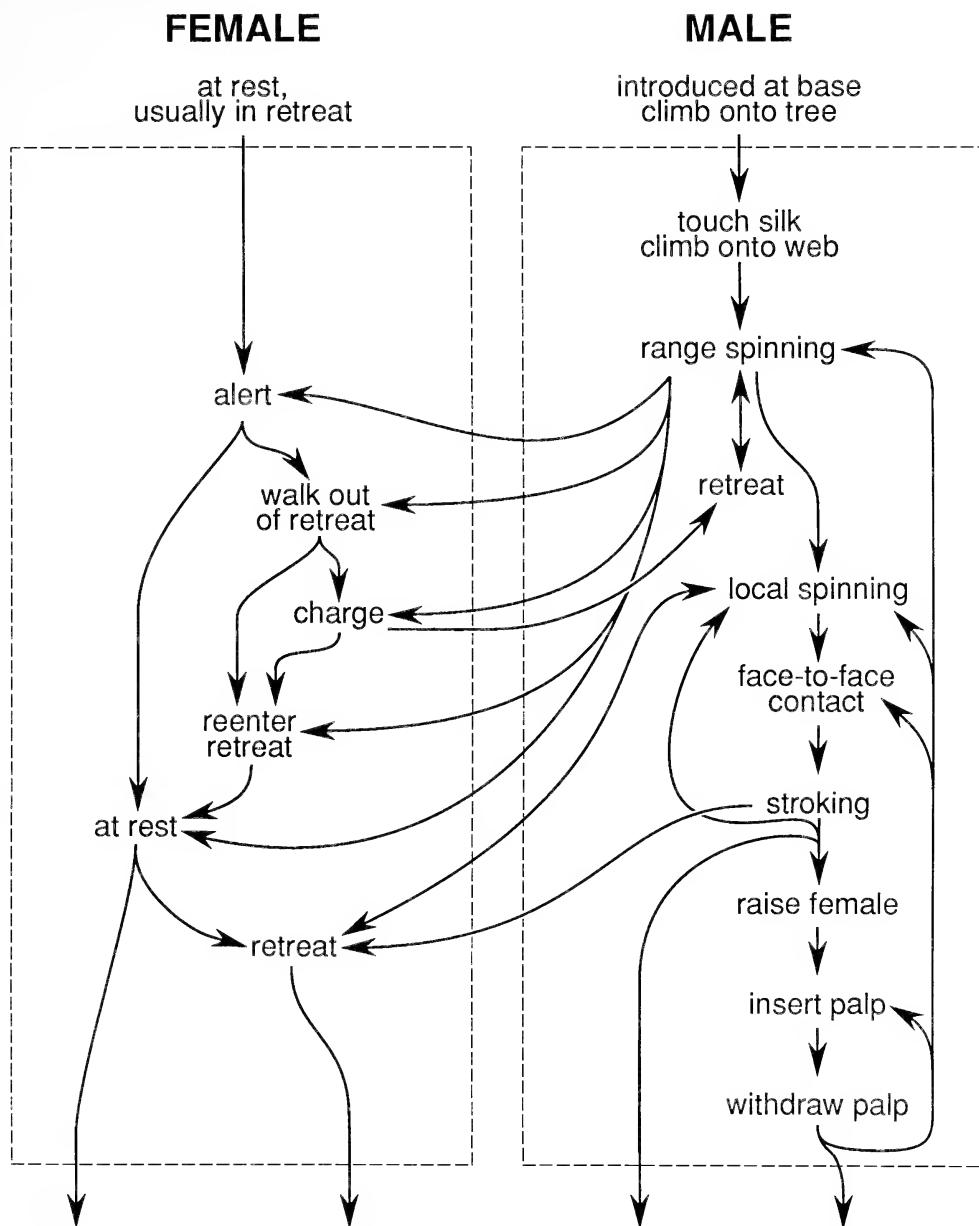


Fig. 5.—Diagram of observed sexual behavioral sequences of *D. volucripes*. Dashed lines delimit sexual behavior.

The sequences of female and male behaviors in *D. volucripes* are shown in Fig. 5. Jackson (1979) divided courtship in dictynids into a non-contact and a contact phase. This division is evident in *D. volucripes*, though I prefer to distinguish three phases. Ranging-spinning is purely a non-contact phase, local-spinning is a transition phase, and the stroking phase is purely a contact phase.

Sperm induction evidently takes place before the start of courtship, as it was not observed in any trial. It appears usual for dictynids to re-induce sperm soon

after mating (Gerhardt and Kaestner 1937; Billaudelle 1957; Bristowe 1971), but we did not see this in *D. volucripes*.

The present results are consistent with Jackson's (1979) conclusion that vision has little or no role in dictynid courtship. The finding that males on recently vacated webs courted normally in the ranging-spinning and first part of the local-spinning phases likewise corroborates his conclusion that it is the female's silk which releases and directs courtship in his "non-contact phase".

Any study of courtship in spiders suffers from the burden that its principal function is not yet established. Despite decades of controversy (for a summary review see Robinson and Robinson 1980), the two main contending hypotheses remain the same: Successful courtship (a) inhibits a very predatory animal (the female) from attacking a very edible one (the male), or (b) stimulates the female to accept the male as a mate. The two hypotheses need not be mutually exclusive, but the question remains of which is the limiting factor in courtship evolution.

The predation-inhibition hypothesis is so attractive that it long had near hegemony among araneologists. For a recent explicit example of this view, see Gertsch (1979). T. H. Savory's repeated protest (e.g., Savory 1928) that sexual approach is in fact rarely hazardous for male spiders seems to have had little impact, possibly because other aspects of his view of courtship are so hard to accept. Recent studies (e.g., Jackson 1979; Robinson and Robinson 1980), however, increasingly support the view that courtship is mainly a matter of female mate-choice. That is to say, it requires little effort to inhibit the female's predatory drive, but much to gain acceptance as a mate. On a larger scale, this is in line with the view of animal courtship as shaped mainly by female choice and not by a need for species-recognition (Thornhill and Alcock 1983; West-Eberhard 1984; Eberhard 1985).

The present study was not made with either hypothesis in mind, but I believe it contributes to this question. I interpret the results as much more consistent with female choice than with a need to inhibit predation. Let me mention in passing that I reach this conclusion reluctantly, as the predation-inhibition hypothesis has always for me invested spider and scorpion courtship with special fascination. In none of the 13 trials was there any indication that the male was in serious danger. Only in a minority of trials did the female rush at or otherwise vigorously approach him, and in each case he easily retreated out of reach.

On the other hand, there were good indications of female choice. In three of 13 trials, normal courtship failed to lead even to a first insertion. In two of eight trials in which the male courted beyond the first insertion, he did not achieve a second insertion. There are further indications of mate-choice in the behavior of females. Females showed much less behavioral variety than males (Fig. 5) and after the initial reaction during ranging-spinning they mostly remained passive in the retreat. In a few cases the female retreated slightly from the male during local-spinning or stroking, apparently in resistance to courtship.

Mate-choice is also implied in raising the female prior to insertion. In the Results and Fig. 5, I treat this as an active process on the male's part and passive on the female's part. Although I cannot be certain of this, it had that appearance, and the first two pairs of legs are surely strong enough to raise another spider's body. At the same time, it seems clear that a female which grasps the substrate silk with flexed legs could not be lifted by force, and females sometimes appeared to resist in this way. In some trials the male was seen to repeatedly reach his legs

Table 1.—Period of hematodocha pulsation in dictynid spiders. Explanation in text. Billaudelle (1957) in fact specified 2-3 pulsations/s in *D. civica*, but I assume he meant one per 2-3 s.

| SPECIES | PERIOD (seconds) | REFERENCE |
|----------------------------------|--|------------------|
| <i>Dictyna benigna</i> | about 4-30 (increasing during time of insertion) | Karpinski 1882 |
| <i>Dictyna civica</i> | 2-3 | Billaudelle 1957 |
| <i>Dictyna sublata</i> | about 6 | Montgomery 1903 |
| <i>Dictyna volucripes</i> | 2-10 (mostly 7-9) | this paper |
| <i>Heterodictyna viridissima</i> | about 10 | Berland 1916 |

under the female's carapace in apparent unsuccessful attempts to raise her. The best interpretation of stroking, then, is that it serves to overcome resistance to raising.

The tendency to revert to courtship between insertions is part of the usual pattern in dictynids (Jackson 1979). The general lack of female aggression and her almost complete passivity at this time make it hard to reconcile such renewed courtship with any need to inhibit predation.

Jackson (1979) has reviewed the durations of insertions reported from dictynids. These are almost all between 15 min and 2 h, much like those recorded from *D. volucripes*. Pulsations of the hematodocha during mating have previously been timed in four species (Table 1). These mostly have a period of 2-10 sec, likewise in the range recorded in *D. volucripes*.

Prolonged cohabitation has been reported from several families of spiders, but seems especially prevalent in the Dictynidae (Bristowe 1971; Gertsch 1979; Jackson 1979). Together with the generally nonaggressive nature of sexual activity, this led Bristowe (1971) to remark on "the unusual friendship which seems to exist between the males and females" in this family. The adaptive basis for such cohabitation is unknown. At present the best hypothesis seems to be that it functions primarily in mate-guarding by males Jackson (1977).

If the function of cohabitation is obscure, its main social-evolutionary implication seems clear. Any mechanism which facilitates mutual tolerance among conspecifics removes a key obstacle to sociality. Cohabitation cannot explain why some dictynids are social, but it shows why they need not be solitary.

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SPIDER FAUNA OF FLOODED RICE FIELDS IN NORTHERN CALIFORNIA

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ABSTRACT

A survey of the spiders associated with northern California rice fields was conducted to identify potential biological-control agents of rice feeding insects and mosquitoes. All of the 28 species were collected on the levees; however, only 10 of these were taken in the paddies. *Pardosa ramulosa* (McCook), *Pirata piraticus* (Clerck) and two linyphiid spp. were common throughout the agroecosystem. These spiders exhibited a seasonal succession in relative abundance within the paddy during the growing season. *Pardosa ramulosa* was dominant both on the levees and in the paddies. It comprised ca. 58 and 68% of the fauna in these respective areas. We suggest that the flooded paddies may serve as a refuge for the semiaquatic *P. ramulosa* during the dry summer months and that its abundance in California rice fields is due in part to the similarity of this agroecosystem to the native, pre-agricultural habitat.

INTRODUCTION

Rice, *Oryza sativa* L., was introduced into California in 1912 and is now grown annually on about 161,880 ha (400,000 acres). Rice production is a major industry in the Sacramento Valley where more than 90% of the rice acreage in the state is located. A rice field is a complex agroecosystem, containing many aquatic, semiaquatic, and terrestrial species. Spiders are well represented among the many predators found in this habitat. They feed mostly on insects and may contribute in reducing pest levels. Lower pest densities have been attributed to spider activity in rice fields of Asia (Kiritani 1979) and other agroecosystems worldwide (Riechert and Lockley 1984).

Numerous surveys of spiders have been conducted in the rice growing regions of Asia (Barrion and Litsinger 1984). However, little is known about spiders associated with rice in the United States. Preliminary surveys have been conducted in Texas (Woods and Harrell 1976) and Arkansas (Heiss and Meisch 1985), but no attempt has yet been made to formally describe the California rice field fauna. This paper identifies the spiders collected from the levees and flooded paddies of several California rice fields over a three year period.

MATERIALS AND METHODS

Sampling began in 1983 at the following locations: the Beck ranch near Modesto (Stanislaus County), Van Dyke ranch near Natomas (Sutter County),

and in the Lattemore seed-field section of the Rice Experiment Station near Biggs (Butte County). Sampling efforts in 1984-1985 were limited to the Biggs site after it was determined the three areas yielded nearly identical results with respect to common species.

The California rice field habitat and associated common vegetation were described by Barrett and Seaman (1980). Notable differences in vegetation among sampling sites used in this study included dense populations of common cattail (*Typha latifolia* L.) and bermuda grass (*Cynodon dactylon* (L.) Pers.) on the levees at the Modesto and Natomas sites, respectively, but not at Biggs. Monochoria (*Monochoria vaginalis* (Burm. f.) Presl.) and toothcup (*Rotala indica* (Willd.) Koehne) were restricted to and abundant in the paddies at the Rice Experiment Station.

Wide mouth Mason jars (11 cm deep and 7.5 cm in diameter) served as pitfall traps. They were inserted into plastic sleeves that were permanently buried in the levees flush with the soil surface. Ten traps were installed at each site at ca. 8 m intervals in an alternating pattern (north side, center, south side, etc.) along the length of a levee in selected fields. One hundred and fifty ml of 95% ethylene glycol plus 5% liquid detergent was added to each trap. After seven days, the traps were collected. The contents were filtered through a USA Standard Testing Sieve No. 40 and stored in 70% EtOH. This procedure was repeated monthly throughout the growing season (May-September).

Floating sticky traps were made by cutting white styrofoam into triangular wedges 61 cm long, 4.5 cm high, with bases of 9 cm. A thin coat of Stickem Special™ (Seabright Enterprises Ltd.; Emeryville, CA) was brushed on the upper surfaces. Five traps were placed in each field and positioned equidistant from one another (ca. 34 to 92 m apart depending on field size) along a transect connecting the NE and SW corners of the field with the end traps being placed 2 m from the margins. They were held in place with green bamboo stakes in a manner that allowed the traps to move vertically so contact with the fluctuating water surface could be maintained. The stakes also served to mark the position of the traps. After seven days, the traps were collected and the spiders identified (to species when possible) with the aid of a 10X hand lens. The sampling schedule was the same as that for the pitfall traps.

Companion samples were taken in 1983 with a UC-VAC® suction device (Summers et al. 1984) to estimate absolute densities and determine the nature and extent of any bias associated with pitfall and sticky-trap sampling. Ten samples ca. 10 m apart were collected both on the levees and in the paddies. A circular unit-area-sampler, enclosing 0.093 m² (1 ft.²) and standing 38 cm (15 in.) high, was placed in the general vicinity of the pitfall and floating sticky traps. The enclosed substrate and vegetation were vacuumed for ca. 90 s. Sampling was conducted between 1200 and 1400 hours. Samples were immediately placed in a cooler with ice for transport, and later processed in Berlese funnels for 48 h.

RESULTS AND DISCUSSION

More than 30,000 specimens were collected in the survey. Species that were taken at all sampling sites in every year—representing 11 families, 22 genera and 28 species—are listed in Table 1. They have been ranked as 4 common, 2

Table 1.—Spiders collected in northern California rice fields (1983-85). a = L, levee; P, paddy. b = R = rare (< 1%); O = occasional (1-5%); C = common (> 5%). Species frequencies determined by averaging counts from UC-VAC (levee) and pitfall-trap samples.

| Taxa | Location ^a | Frequency ^b |
|--|-----------------------|------------------------|
| Dysderidae | | |
| <i>Dysdera crocata</i> C. L. Koch | L | R |
| Linyphiidae Erigoninae | | |
| Species A | L,P | C |
| Species B | L,P | C |
| Araneidae | | |
| <i>Araneus trifolium</i> (Hentz) | L,P | R |
| <i>Argiope aurantia</i> Lucas | L,P | R |
| <i>Argiope trifasciata</i> (Forsk.) | L,P | R |
| Tetragnathidae | | |
| <i>Tetragnatha elongata</i> Walckenaer | L,P | R |
| <i>Tetragnatha laboriosa</i> Hentz | L,P | R |
| Lycosidae | | |
| <i>Alopecosa kochi</i> (Keyserling) | L | R |
| <i>Pardosa ramulosa</i> (McCook) | L,P | C |
| <i>Pirata piraticus</i> (Clerck) | L,P | C |
| Oxyopidae | | |
| <i>Oxyopes salticus</i> Hentz | L | R |
| Gnaphosidae | | |
| <i>Drassyllus insularis</i> (Banks) | L | R |
| <i>Drassyllus saphes</i> Chamberlin | L | R |
| <i>Micaria</i> sp. | L | R |
| <i>Trachyzelotes lyonneti</i> (Audouin) | L | R |
| <i>Urozelotes rusticus</i> (L. Koch) | L | R |
| <i>Zelotes puritanus</i> Chamberlin | L | R |
| Thomisidae | | |
| <i>Xysticus californicus</i> Keyserling | L | R |
| Philodromidae | | |
| <i>Tibellus oblongus</i> (Walckenaer) | L,P | O |
| Salticidae | | |
| <i>Habronattus klauserii</i> (Peckham & Peckham) | L | R |
| <i>Metaphidippus vitis</i> (Cockerell) | L | R |
| <i>Neon ellamae</i> Gertsch & Ivie | L | R |
| <i>Phidippus californicus</i> Peckham & Peckham | L | R |
| <i>Phidippus clarus</i> Keyserling | L | R |
| <i>Phidippus johnsoni</i> (Peckham & Peckham) | L | R |
| <i>Sitticus dorsatus</i> (Banks) | L | R |
| Dictynidae | | |
| <i>Tricholathys saltona</i> Chamberlin | L | O |

occasional and 22 rare species. All 28 species were collected on the levees (including vegetation) but, only 10 of the species were taken in the paddy. Apparently many of the levee species were incapable of inhabiting an aquatic microhabitat. Only four species—*Pardosa ramulosa* (McCook), *Pirata piraticus* (Clerck) and two linyphiid spp.—were common in the paddy. Other spider species occasionally found in the paddy were generally limited to the paddy margins late in the growing season after the crop canopy had filled in enough to allow plant-to-plant movement and provide adequate sites for web attachment. The four common paddy spiders also dominated the levee fauna.

The number of taxa recorded are generally lower than those reported for other surveys (Paik and Kim 1973). This can be attributed in part to our exclusion of

Table 2.—Relative abundance in percent composition of the major spiders in northern California rice fields. a = 1983; b = Pitfall or sticky-trap catches from 1983-1985.

| Taxa | Levee | | Paddy | |
|-------------------------|------------------------------------|--------------------------------------|----------------------------------|-------------------------------------|
| | UC-VAC ^a (n = 1,099) | Pitfall ^b (n = 16,311) | UC-VAC ^a (n = 614) | Sticky ^b (n = 12,124) |
| Linyphiid spp. | 12.9 | 3.4 | 19.3 | 5.1 |
| <i>Pirata piraticus</i> | 8.4 | 4.0 | 11.4 | 6.4 |
| <i>Pardosa ramulosa</i> | 57.7 | 75.2 | 67.5 | 87.4 |
| Others | 21.0 | 17.4 | 1.8 | 1.1 |

transient species (species not collected at every sampling site in every year, usually represented by a single specimen). Even so, comparisons of this type may be misleading, as great differences exist among the surveys in terms of the extent and methods of sampling. For example, Woods and Harrell (1976) collected 752 specimens from a single 14.8 ha (37 acre) field during one growing season. In contrast, Barrion and Litsinger (1984) collected 13,270 specimens from 17 localities over three years, and Okuma (1968) collected 1,487 spiders from 22 localities during a 10 day period. Furthermore, Heiss and Meisch (1985) sampled with an aquatic net and metal dipper but Okuma and Wongsiri (1973) utilized a sweep net and observations.

In spite of these differences, three families: Araneidae, including Tetragnathidae; Linyphiidae, including the Erigoninae (Micryphantidae) and Lycosidae dominated the spider fauna in all but one of the surveys of rice fields cited in this paper. In addition, the relative abundances of these families changed with latitude. In semitropical rice-growing areas, such as Taiwan, Thailand and the Philippines, araneids dominated (Okuma 1968; Chu and Okuma 1970; Okuma and Wongsiri 1973; Barrion and Litsinger 1984) while lycosids were more abundant in temperate regions such as Korea and the United States (Paik and Kim 1973; Woods and Harrell 1976; Heiss and Meisch 1985; present study). Lycosids and araneids were also abundant in the rice fields surveyed in Japan, although the fauna was dominated by two theridiid spp. (Paik and Kim 1973).

Pardosa ramulosa was dominant in numbers on the levees and in the paddies (Table 2). It comprised ca. 58 and 68% (UC-VAC samples) of the fauna in these respective areas. The two lycosids, *Pardosa ramulosa* and *Pirata piraticus*, together constituted ca. 80% (UC-VAC samples) of the paddy spiders. They appeared to be well adapted to the water surface where they quickly ran about or remained motionless for long periods. They occasionally went underwater by crawling down emergent vegetation or debris. Other paddy spiders, although capable of limited locomotion on the water surface, spent most of their time on vegetation or in webs constructed among the paddy plants. Linyphiids were also seasonally abundant. However, their contribution to total spider biomass over the growing season was relatively small, compared to that of the common lycosids, because of their small size and ephemeral occurrence.

Sticky and pitfall-trap samples probably overestimated *Pardosa ramulosa* while underestimated linyphiids and *Pirata piraticus* abundances compared to UC-VAC samples (Table 2). Although fewer spiders were collected with the UC-VAC, these data were probably more accurate in estimating relative abundances for the major species. The UC-VAC was not used more extensively because of the much greater

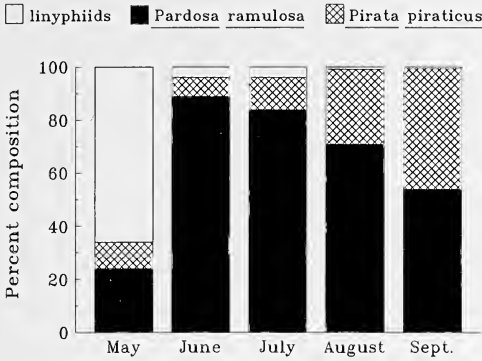


Fig. 1. Relative seasonal abundance of the major paddy spiders in northern California rice fields for 1984 (sticky-trap catches).

relative time and effort it required. Foliage dwelling species such as *Tibellus oblongus* (Walckenaer) were only collected with the UC-VAC whereas nocturnal ground dwellers such as the dictynids and gnaphosids were limited to pitfall traps. This illustrates the importance of utilizing multiple collecting techniques in faunal surveys of spiders.

The major paddy spider species exhibited a seasonal succession in relative abundance during the growing season (Fig. 1). The linyphiids dominated the spider fauna in the paddies shortly after flooding. Their abundance was associated with the spring ballooning period when they arrived in massive numbers. Unlike the other two major paddy species, the linyphiids do not appear to be specifically adapted for, or restricted to, aquatic environments.

Pirata piraticus is distributed throughout Europe and north of the 35th parallel in North America. It is associated with swamps, marshes and the shores of lakes, ponds and streams (Wallace and Exline 1977). It became a major component of the paddy fauna late in the growing season.

Pardosa ramulosa is found throughout California. Its range extends E through southern Nevada into the SW corner of Utah and S into northern Mexico. In California it is one of the dominant lycosids at elevations below 300 m (Hydorn 1977). It is associated with mesic habitats such as salt marshes (Garcia and Schlinger 1972; Greenstone 1980), sewage oxidation ponds (Hydorn 1977), irrigated lawns (Van Dyke and Lowrie 1975) and irrigated crops (Leigh and Hunter 1969; Yeargan and Dondale 1974; Hickie 1981). The prevalence of *P. ramulosa* in rice and other irrigated crops in California is probably related to the seasonal compression of suitable habitat. As drying begins in the spring and continues through the summer these spiders are probably forced to aggregate where moist conditions persist. Irrigated cropland, particularly rice, which is typically continuously flooded from May through September, offers such a refuge. Rice culture in California resembles the native habitat of some areas that existed before the advent of flood control and irrigation projects when many parts of the Sacramento and San Joaquin Valleys were annually flooded from snowmelt. Rice fields probably represent the functional equivalent of the numerous vernal ponds and marshes that were presumably utilized by *P. ramulosa* in its pristine environment, but differ by extending moisture availability, which is essential for this species (Hydorn 1977), throughout the summer. For a large part of the growing season, this native natural enemy is actually favored by, and more abundant in, rice (an introduced annual crop) than in adjacent untilled

border areas (Oraze et al. unpublished data). Because of its abundance in, and preadaptation to, the rice field environment, *Pardosa ramulosa* appears to be the spider most likely to contribute to a level of biological control of one or more insect pests in this agroecosystem. The impact of this spider on selected prey species in rice will be presented in a subsequent paper (Oraze and Grigarick 1988).

Our sampling did not include any wild rice (*Zizania aquatica* L.) fields. This crop supports more vegetative growth and is usually produced earlier in the year (February-July) than conventional rice. We suspect that these cultural differences may cause minor differences in the respective spider faunas, and a comparative study would be of value.

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FOUR NEW SPECIES OF *PARATHEUMA* (ARANEAE, DESIDAE) FROM THE PACIFIC

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ABSTRACT

Four new species of *Paratheuma* are described from the Cook, Fiji and Tuamotu Islands and Australia. New records of *P. armata* are presented. Possible relationships among species of the genus are suggested.

INTRODUCTION

In a recent paper (Beatty and Berry 1988) we illustrated and discussed the three known species of the genus *Paratheuma* Bryant. Here we report the rather surprising subsequent discovery of four new species of the genus from Australia and the Cook, Fiji and Tuamotu Islands of the South Pacific.

Like the other species, these were taken near the high tide level on seashores, often among loose broken coral thrown up on the beach. However, we found some individuals under large non-coralline rocks, and others in crevices or holes in outcrops of volcanic or conglomerate rocks a few cm to about one meter above normal high tide level.

The previously known species of *Paratheuma* are *P. insulana* (Banks) from Bermuda, Florida, Cuba and Haiti (Banks 1902, 1903; Beatty and Berry 1988; Bryant 1940; Platnick 1977), *P. interaesta* (Roth and Brown) from the northern part of the Gulf of California (Beatty and Berry 1988; Platnick 1977; Roth and Brown 1975), and *P. armata* (Marples) from Swains Island, Marshall Islands and Caroline Islands in the Pacific (Beatty and Berry 1988; Marples 1964). The four new species are quite similar to these in size, shape, coloration and setation, as well as habitat.

We have already described (Beatty and Berry 1988) the range of coloration in the genus, and the additional species add little to this range. A few of the recently collected specimens, almost black on the abdomen, are darker than any we had

seen earlier. The light abdominal chevrons occasionally present are more distinct in some specimens than our previous description suggests.

Size and proportions of all species show so little variation that we have presented only a few measurements in the descriptions below. Three adult males and three adult females of each species were measured, except for *P. andromeda*, of which we had only one male.

We have not described the bristle pattern for each species individually, largely because the bristles are weak, not very abundant, and vary little among species. Instead, a separate description is presented, which applies equally well to all the Pacific species. These "bristles" are, of course, setae, but the presence of three main size classes of setae in spiders makes retention of the commonly used terms, "hairs, bristles and spines" useful for distinguishing among them.

DESCRIPTIONS

Setation.—All five of the Pacific *Paratheuma* have the same arrangement of bristles, with no more variation among the species than within a single population of one of them. There is almost no difference in the pattern between males and females. In the following description a bristle number indicated as 1-3 means one to three bristles; 1-2-3 means one proximal bristle, two near mid-length, and three distal, on a particular appendage surface.

Palp.—Two dorsal bristles on femur, in distal half; two dorsal on patella, one proximal, one distal; two prolateral and one dorsal on tibia; on tarsus, two prolateral and two retrolateral near base (the retrolateral pair absent in adult males), a pair just distal to mid-length of tarsus, one on each side, another such pair at distal end, and two distal ventral bristles in the mid-line.

Legs.—*Femora*: In both sexes on all legs, 1-3 dorsal, 1 dorsolateral. Dorsolateral bristle dorsoprolateral on legs I-II, dorsoretrolateral on III-IV. *Patellae*: Two dorsal (one proximal, one distal) on all legs in both sexes. *Tibiae*: Leg I, 1-2 dorsal, 2-3 ventral. Leg II, 2 dorsal, 1 prolateral, 2 ventral. Leg III, 1-(0-2)-3 dorsal, 1-1-1 ventral. Leg IV, 1-2-3 dorsal, (1-2)-(1-2)-(1-3) ventral. *Metatarsi*: Legs I and II, 5-6 ventral arranged (1-2)-2-2. Leg III, (0-1)-2-2 dorsal, 2-2-3 ventral. Leg IV, 2-2-2 dorsal, 2-2-3 ventral.

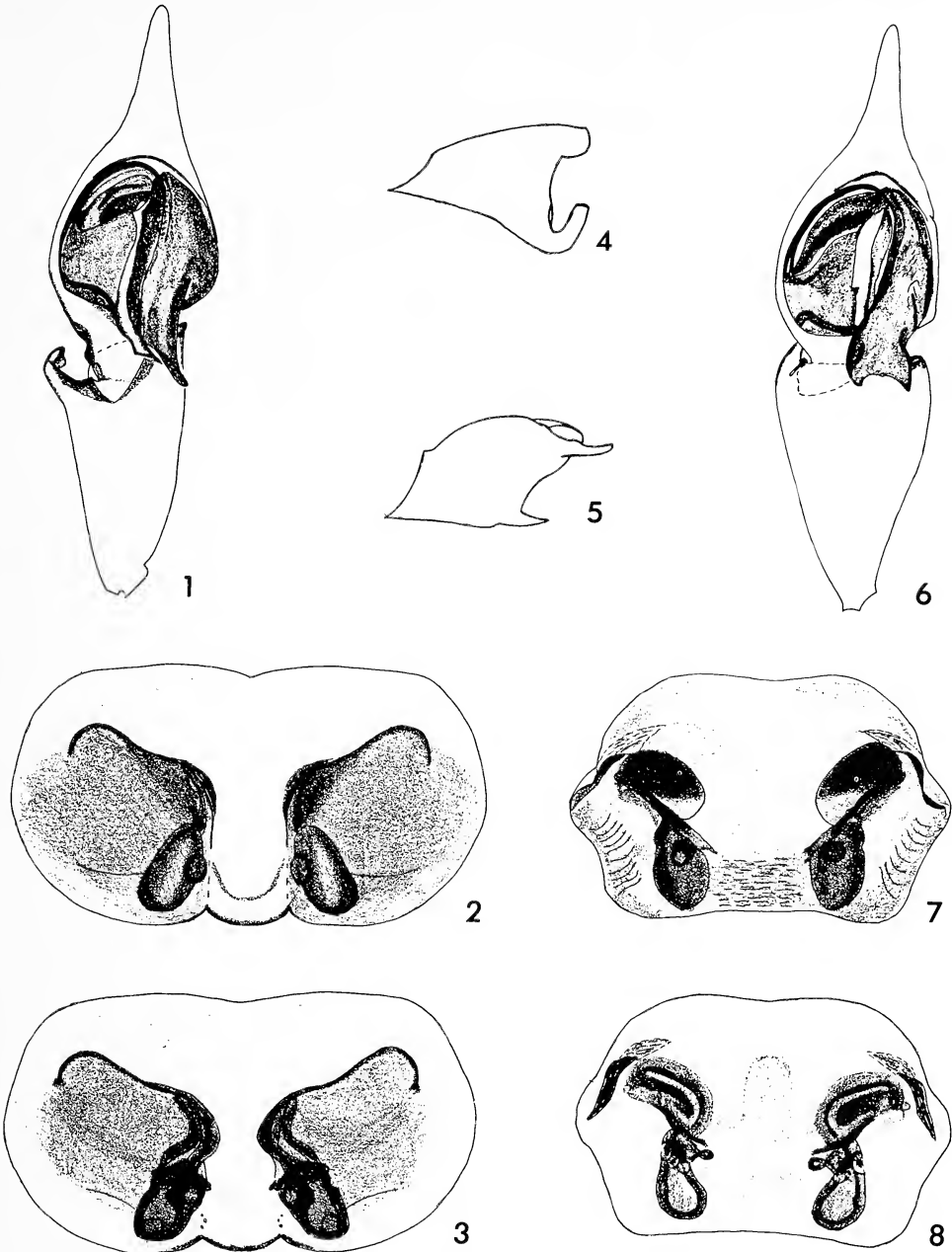
Juvenile specimens listed below are not to be regarded as paratypes. Holotype males and one paratype female of each species are deposited in the Bishop Museum, Honolulu. All other material examined remains in the possession of the authors.

Paratheuma andromeda, new species

Figs. 1-4

Holotype.—Male from Cook Islands, Aitutaki, Rapota Motu, in crevice in volcanic rock outcrop on shore, 5 June 1987 (J. W. Berry), in Bishop Museum, Honolulu, Hawaii, USA. The name *andromeda* is a noun in apposition after Andromeda of classical mythology.

Diagnosis.—Male: The broad tibial apophysis of the male palp, curving dorsally and toward the cymbium (Fig. 4) clearly distinguishes *andromeda* from



Figs. 1-8.—Left male pedipalp and epigynum of *Paratheuma* species: 1-4, *P. andromeda* from Aitutaki, Cook Islands; 1, pedipalp, ventral; 2, epigynum, ventral; 3, epigynum, cleared, dorsal; 4, tibia of pedipalp, lateral; 5-8, *P. ramseyae* from Rarotonga, Cook Islands; 5, tibia of pedipalp, lateral; 6, pedipalp, ventral; 7, epigynum, ventral; 8, epigynum, cleared, dorsal.

all other species of the genus. The length and orientation of the distal processes of the conductor (Fig. 1) are also distinctive.

Female: The large ovate seminal receptacles distinguish this species from all others except *P. ramseyae*. From the latter *andromeda* differs by having the entire

anterior margin of the epigynal depressions sclerotized, and by lacking the heavily sclerotized pouch around the epigynal openings (Figs. 2-3).

Additional descriptive notes.—Male: Total length 3.8 mm, carapace length 1.7 mm, maximum carapace width 1.1 mm. Embolus originating at mid-length of bulb, curving around anteromedial margin of bulb, turning back to end in hairfine filament on conductor. Two rather long narrow distal processes of conductor almost parallel with long axis of tibia, curving slightly laterally (Fig. 1). Tibial apophysis of palp broad, curving strongly dorsally and toward cymbial base (Fig. 4).

Female: Total length 4.1-4.4 mm, carapace length 1.7-1.8 mm, maximum carapace width 1.2-1.3 mm. Epigynum with narrow sclerotized rim along entire anterior length of depressions, curving short distance along lateral margin. Broad heavily sclerotized ducts leading from openings to large ovate seminal receptacles.

Distribution.—Known only from a small area of volcanic shoreline on one islet of Aitutaki, Cook Islands, and from the shore of a nearby islet. The apparently very restricted distribution of this species is unusual for the genus, though it is possible that it occurs on other main islands of the Cook group. A large percentage of the shoreline of the Aitutaki Islands was searched, without success, for additional specimens.

Specimens examined.—**COOK ISLANDS:** *Aitutaki*; Moturakau, in coral rubble on beach, 28 March 1987 (J. W. Berry), 1 female, 1 immature; Rapota Motu, in crevices and holes in volcanic and conglomerate rock at shoreline, 5 June 1987 (J. W. Berry), 1 male, 2 females.

Paratheuma ramseyae, new species

Figs. 5-8

Holotype.—Male from Cook Islands, Rarotonga, Koromiri Islet, in broken coral rubble on beach, 3 April 1987 (J. W. and E. R. Berry), in Bishop Museum, Honolulu, Hawaii, USA. The species is named after Elizabeth Ramsey Berry, who discovered it.

Diagnosis.—Male: Distal end of conductor broad, with two short, bluntly pointed processes that curve slightly toward tibia (Fig. 6). Tibial apophysis slender, curving dorsally and toward cymbium (Fig. 5).

Female: Distinguished from all other species by the short anterolateral sclerotizations of the epigynal depressions, and the large hoodlike sclerotized pouches around the epigynal openings (Figs. 7-8).

Additional descriptive notes.—Male: Total length 3.3-3.9 mm, carapace length 1.6-1.8 mm, maximum carapace width 1.2-1.3 mm. Embolus of palp as in other species described here. Other palpal characters as in diagnosis.

Female: Total length 3.6-4.5 mm, carapace length 1.7-1.8 mm, maximum carapace width 1.3 mm. Sclerotizations of rim of epigynal openings short and sigmoid, located in anterolateral portions of depressions only. Openings leading into large sclerotized pouches. Short ducts from pouches to large ovate seminal receptacles.

Distribution.—Cook Islands, Rarotonga. Known from the main island of Rarotonga itself, and from four small islets inside the fringing reef.

Specimens examined.—**COOK ISLANDS:** *Rarotonga*; Ngatangia Harbor beach, in rock outcrops, 31 March 1987 (J. W. Berry and J. A. Beatty), 1 female, 1 immature; Koromiri Islet, in broken coral rubble on sand beach, 3 April 1987 (J. W. Berry and E. R. Berry), 2 males, 1 female, 8 immature;

Koromiri Islet, in coral rubble, 4 April 1987 (J. W. and E. R. Berry), 1 male, 1 female, 5 immature; Koromiri Islet, in coral rubble, 6 April 1987 (J. W. and E. R. Berry), 3 females, 28 immature; Oneroa Islet, in beach litter, 21 March 1987 (J. W. and E. R. Berry), 1 female, 2 immature; Taakoka Islet, in crevices on volcanic rock outcrop at shore, 19 March 1987 (J. W. Berry and J. A. Beatty), 1 male, 2 females; on offshore islets at Muri Beach, 27 March-1 April 1987 (J. W. and E. R. Berry), 3 males, 1 female, 3 immature.

Paratheuma australis, new species

Figs. 9-12

Holotype.—Male from Fiji, Viti Levu, Korotongo village, shoreline at Reef Resort, in coral rubble, 21 May 1987 (J. W. Berry and E. R. Berry), in Bishop Museum, Honolulu, Hawaii USA. The name *australis* is an adjective based upon the more southern range of this species, compared with most others in the genus, and its occurrence in Australia.

Diagnosis.—Male: Palp with slender erect tibial apophysis of medium length, as in *P. insulana* and *P. rangiroa*. Distinguished from *insulana* by its broader cymbium and palpal bulb, from *rangiroa* by the more anteriorly directed tibial apophysis and the shape of the conductor tip.

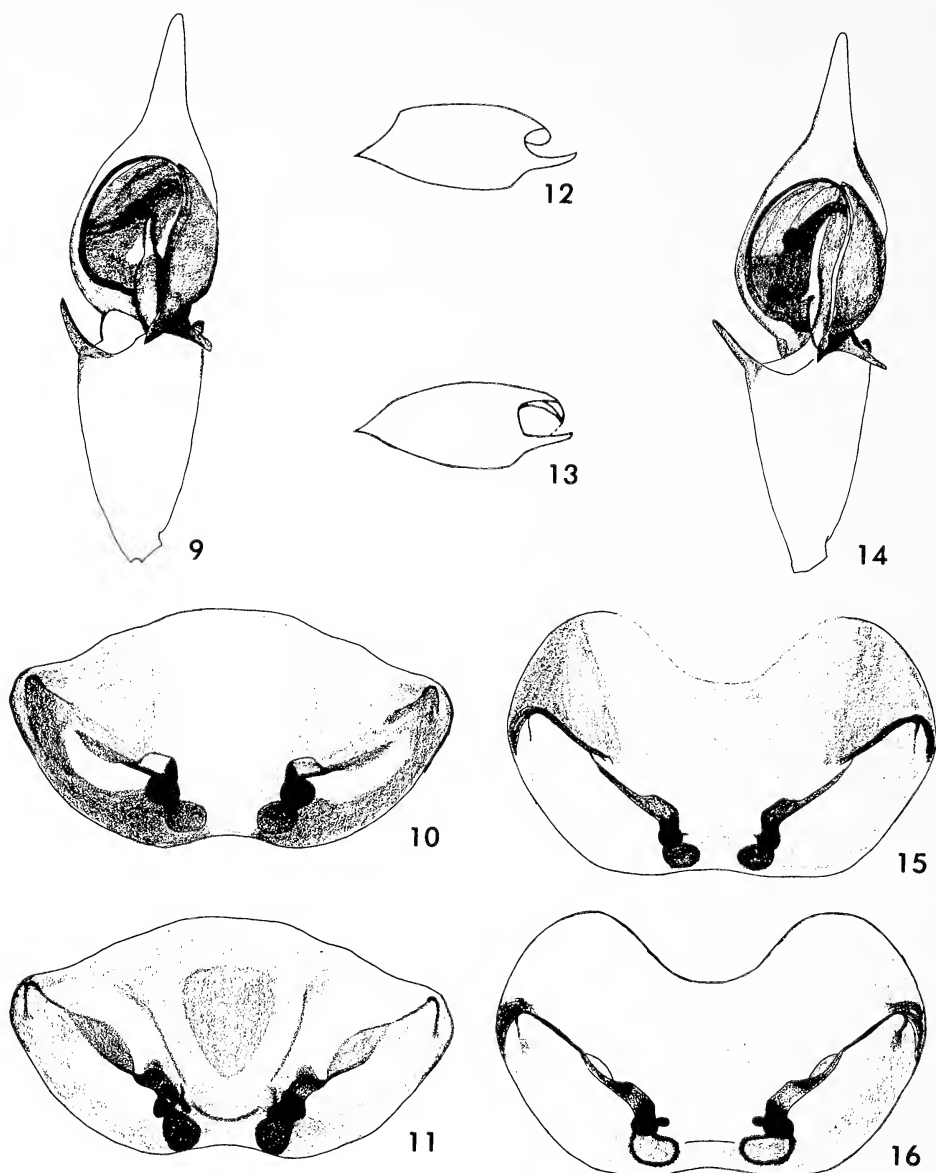
Female: With narrow oblique epigynal depressions, as in *P. insulana* and *P. rangiroa*. Distinguished from *insulana* by reduction of the anterolateral hoods of the epigynal depressions. See discussion under *P. rangiroa* for differences from that species.

Additional descriptive notes.—Male: Total length 3.2-3.5 mm, carapace length 1.5-1.7 mm, maximum carapace width 1.1 mm. Embolus originating on medial side of bulb near mid-point of bulb's length, slender, tapering, curving in broad parabola to end in filament lying under edge of conductor. Tibial apophysis about 1/5th length of cymbium, directed forward at slight angle to axis of tibia, slender and curving slightly dorsally (Fig. 12). End of conductor broad, extended into two angular processes, one directed backward and slightly medially, one longer, extending laterally (Fig. 9).

Female: Total length 3.4-4.2 mm, carapace length 1.5-1.7 mm, maximum carapace width 1.0-1.1 mm. Epigynal depressions pale, extending obliquely forward and laterally, with only short narrow sclerotized rim anterolaterally. Openings at anterior medial edge of depressions, leading to short looped ducts ending posteriorly in pair of small receptacles (Figs. 10-11).

Distribution.—Fiji Islands and Australia.

Specimens examined.—AUSTRALIA: QUEENSLAND: Great Keppel Island, Leek's Beach, in coral rubble, 24 April 1987 (J. W. and E. R. Berry), 2 males; Monkey Beach, in coral rubble, 24 April 1987 (J. W. Berry), 4 immature; Yeppoon, Wave Point, among granitic rocks on beach, 23 April 1987 (J. W. and E. R. Berry), 1 male, 2 females, 7 immature. FIJI: Viti Levu; Nadi, Nadi Bay, in beach rubble, 29 April 1987 (J. W. and E. R. Berry), 1 male, 1 female; Nadi Bay, in gravel on beach (J. W. and E. R. Berry), 1 male, 4 immature; 2 km W of Vatukarasa, on beach among small coral rocks, 12 May 1987 (J. W. Berry), 1 female; Korotongo village, shore at Reef Resort, in coral rubble, 21 May 1987 (J. W. and E. R. Berry), 2 males, 2 females, 6 immature; 0.5 km E of Komave village, in coral rubble on beach, 24 May 1987 (J. W. and E. R. Berry), 1 male, 2 females, 21 immature.



Figs. 9-16.—Left male pedipalp and epigynum of *Paratheuma* species: 9-12, *P. australis* from Viti Levu, Fiji Islands; 9 pedipalp, ventral; 10, epigynum, ventral; 11, epigynum, dorsal, cleared; 12, tibia of pedipalp, lateral; 13-16, *P. rangiroa* from Rangiroa, Tuamotu Islands; 13, tibia of pedipalp, lateral; 14, pedipalp, ventral; 15, epigynum, ventral; 16, epigynum, cleared, dorsal.

Paratheuma rangiroa, new species

Figs. 13-16

Holotype.—Male from Tuamotu Islands, Manihi, Topihairi Islet, in beach rubble, 3 June 1987 (E. R. Berry), in Bishop Museum, Honolulu. The name is a noun in apposition after the atoll where the species was first found.

Diagnosis.—Male: Palp with slender erect tibial apophysis of medium length, as in *P. insulana* and *P. australis*. Distinguished from *insulana* by its broader

cymbium and palpal bulb, from *australis* by the more laterally directed tibial apophysis and the shape of the conductor tip, the medial projection of which is smaller and the lateral projection longer than in *australis*.

Female: With narrow oblique epigynal depressions as in *P. insulana* and *P. australis*. Distinguished from *insulana* by reduction of the anterolateral hoods of the epigynal depressions, from *australis* by the longer sclerotized rim of the depressions and the somewhat larger and more oblong seminal receptacles.

Discussion: This species is genitally quite similar to *P. australis*. It is smaller than *australis*, and the genitalic differences, though slight, are constant in the available material. The presence of three more quite distinct species of the genus on islands between the ranges of *rangiroa* and *australis* argues for their distinctness. Comparison of these two species by electrophoresis of proteins from whole body extracts (Laemmli 1970, for method) showed clear differences.

Additional descriptive notes.—Male: Total length 2.7-2.8 mm, carapace length 1.3-1.4 mm, maximum carapace width 0.9-1.0 mm. Palp as in *P. australis* except for differences noted in diagnosis (Figs. 13-14).

Female: Total length 3.1-3.7 mm, carapace length 1.4-1.6 mm, maximum carapace width 1.0-1.1 mm. Epigynum as in *P. australis* except for differences noted in diagnosis (Figs. 15-16).

Distribution.—Known only from Rangiroa and Manihi Atolls in the Tuamotu Islands of French Polynesia.

Specimens examined.—FRENCH POLYNESIA: Tuamotu Islands; Rangiroa Atoll, on lagoon beach near airport, 17 January 1987 (J. W. and E. R. Berry), 1 female, 1 immature; Avatorua Islet, in beach rubble, 5 June 1987 (E. R. Berry), 1 male, 10 females, 18 immature; Manihi, Topihairi Islet, 3-4 June 1987 (E. R. Berry), 6 males, 3 females, 23 immature.

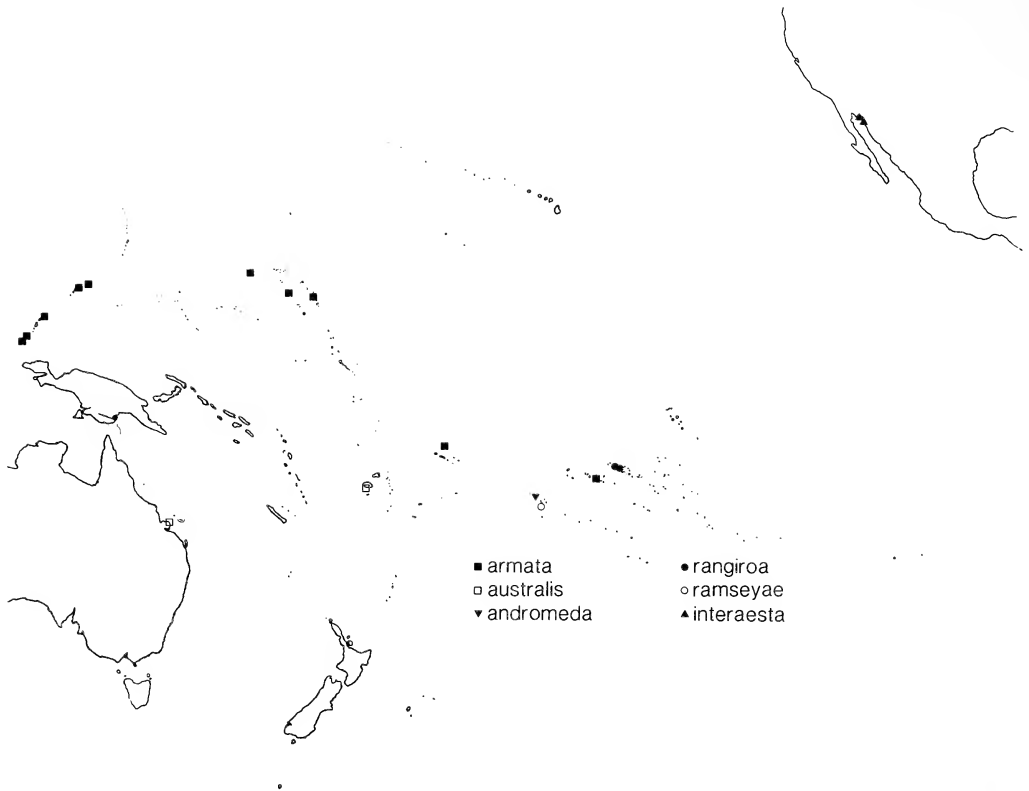
Paratheuma armata (Marples)

New records.—FRENCH POLYNESIA: SOCIETY ISLANDS; *Moorea*, Paopao village, in intertidal coral rubble, 10 January 1987 (J. W. Berry), 1 male, 1 female, 5 immature; Paopao village, in coral rubble on beach (E. R. Berry), 2 males, 6 females; Paopao village, beach rubble, 19 February 1987 (J. W. and E. R. Berry), 2 males, 4 immature; Paopao village, beach rubble, 22 February 1987 (J. W. Berry), 1 male, 2 females; west side of *Moorea*, in pile of supratidal rocks along shore, 13 January 1987 (J. W. and E. R. Berry), 2 males, 7 immature; *Tahiti*, Faai, in coral rubble on beach, 20 February 1987 (J. W. and E. R. Berry), 7 immature; Faai, in coral rubble on beach, 9 June 1987 (J. W. and E. R. Berry), 1 male.

SPECIES RELATIONSHIPS

We are not familiar enough with other members of the family Desidae to select a genus as the probable nearest relative of *Paratheuma*. (Also, the contents of the family seem not clearly determined at present). Consequently we do not feel justified in identifying specific character states as primitive or derived.

Within the genus, *australis* and *rangiroa* appear to be the most closely related pair of species, and both are rather similar to *insulana* from the Caribbean. This suggests a vicariant relationship between *insulana* and the pair of Pacific species. As judged by female genitalia, *andromeda* and *ramseyae* seem close to each other, as would be expected by their geographic proximity. The other two species, *armata* and *interaesta*, are more distinctive and do not appear to have any close relatives among the known species of the genus.



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Fig. 17.—Distribution of *Paratheuma* species in the Pacific.

The distributions of all known Pacific species of *Paratheuma* are entirely on or extend only slightly beyond the borders of the Pacific crustal plate (Fig. 17). Given the usually accepted view that all the islands on this plate have always been highly isolated, dispersal must have been of primary importance in the evolutionary history of the Pacific *Paratheuma*. Judging from our recent experience, however, there is a strong possibility that several, perhaps many, more species of the genus await discovery, and their distribution and characters may change our interpretation of their relationships and history considerably.

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FACTORS INFLUENCING SPECIFICITY AND CHOICE OF HOST IN *ARGYRODES ANTIPODIANA* (THERIDIIDAE, ARANEAE)

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ABSTRACT

The spider *Argyroides antipodiana* (O.P. Cambridge) from New Zealand is a kleptoparasite whose primary host in nature is an orb weaving spider, *Aranea pustulosa* (Walckenaer). The kleptoparasite's bias towards this host is stronger in the summer than in the winter. In the laboratory, *Argyroides* was significantly better at obtaining food on the webs of *Aranea pustulosa*, than on the webs of *Achaearanea* sp., and *Badumna longinquus* (L. Koch). Factors that may be responsible for host preferences and for variation in efficiency on different types of webs are discussed.

INTRODUCTION

Argyroides, a large cosmopolitan genus of theridiid spiders, is notorious for its kleptoparasitic species (Kullmann 1959; Vollrath 1979, 1979a,b; Smith Trail 1980; Rypstra 1981; Wise 1982; Larcher and Wise 1985; Whitehouse 1986). Instead of building prey-capture webs as do most theridiid spiders, *Argyroides* roams through the periphery of other spiders' webs gleaning trapped insects from the silk, pilfering wrapped food bundles directly from the resident spider (host), and sometimes attacking and eating the host.

Vollrath (1984) suggested that *Argyroides* can be loosely classified into two groups: Generalists and Specialists. Generalists invade a wide variety of web-types but use only a few techniques to obtain food; while specialists invade the webs of only a few species and use several techniques to obtain food. To be a specialist, *Argyroides* often needs to respond opportunistically to the host's movements, as it frequently feeds with the host or steals food bundles the host is guarding. Thus a specialist's ability to choose the appropriate host is very important.

Argyroides antipodiana (O.P. Cambridge) (hereafter referred to as *Argyroides*) is a kleptoparasitic spider from New Zealand. The behavioral repertoire of this spider is that of a specialist (Whitehouse 1986). Casual field observations made during the course of this earlier study suggested that *Argyroides* tends to be highly restricted in its host-choice.

The aims of this paper are to present more precise information on the host-choice of *Argyroides* and to investigate possible reasons for restricted host-choice by this species.

METHODS

Field surveys of hosts of *Argyrodus*.—Two surveys, one in early winter, May (approx. average daily temperature range = 4–15°C) 1984, the other in summer, January (approx. average daily temperature range = 15–25°C) 1985, were undertaken at Te Aroha (North Island, New Zealand: 37.32°S; 175.43°E) by examining all the webs in the sample area (ca. 50 m²), collecting any *Argyrodus* found, and recording the types of web on which they were found.

A casual survey was conducted in late winter/early spring, August (approx. average daily temperature range = 5–15°C) 1985, where the author walked over the sample area and noted the sex and maturity of the population.

Laboratory analysis.—Spiders were maintained and tested in transparent plastic cages in a laboratory with controlled light (12:12, L:D) and temperature (20°C–25°C) (for details see Jackson 1974).

Locomotion on webs: Spider webs can be divided into three categories: cribellate webs, which are sticky because they are covered by very fine strands of silk; non-cribellate sticky webs, the glue of which consists of droplets of a sticky fluid; or non-cribellate non-sticky webs which have no glue (see Foelix 1982). *Argyrodus* was placed onto the three types of webs and its locomotion observed.

Mortality on webs: Adult and sub-adult *Argyrodus* were housed upon the established webs of host species *Badumna longinquus* (L. Koch) (Amaurobiidae), *Achaeearanea* sp. (Theridiidae) and *Aranea pustulosa* (Walckenaer) (Araneidae) (hereafter referred to as “*Badumna*”, “*Achaeearanea*”, and “*Aranea*” respectively), until the *Argyrodus* were eaten, they died of natural causes, or the time period for the experiment was completed (the experiment ran for 27 days). Each host was used once only, except for one *Badumna* which was used twice. *Badumna* built cribellate sticky space webs, *Achaeearanea* built non-cribellate sticky space webs, while *Aranea* built non-cribellate sticky orb webs. The spiders were fed every 1–4 days. I recorded the length of time each *Argyrodus* survived on hosts’ webs, and the number of *Argyrodus* that were killed by the hosts. Survival, measured as spider-days of exposure (the number of days *Argyrodus* were exposed to the host) was compared among host species using survival rate analysis (Johnson 1979; Harris et al. in prep.).

Comparison of the capture efficiency of *Argyrodus* on the webs of three host species: Host species *Aranea*, *Achaeearanea*, and *Badumna* of a similar size (ca. 7 mm) were collected and housed in cages suitable for their web-type. The hosts were given ca. 10 days to establish a web before a subadult (i.e., a spider one molt before maturity) or adult *Argyrodus* (body length: ca. 3 mm) was introduced to the cage. At 1–4 day intervals a test was started by dropping 10–20 *Drosophila melanogaster* (Meigen) (fruit flies) onto the host’s web, then 30 min later dropping another 10 fruit flies onto the web (a variable time scale was used to avoid host satiation as satiated hosts are less likely to construct webs). I recorded whether or not *Argyrodus* obtained food during a 2 h test period. If the host’s web did not retain five or more flies, the results were discarded as at this level of prey availability I deemed it too difficult for *Argyrodus* to obtain food. Each test was assumed to be independent of each other as the *Argyrodus* were responding to new conditions. For instance, the time between tests had enabled the host to reconstruct its web and the distribution of restrained flies on the web varied greatly between tests.

RESULTS

Hosts of *Argyroides* in nature.—Only juvenile *Argyroides* were discovered during winter. Of the 133 found, 59% were associated with araneid webs (Table 1). Besides being on or near the araneid orbs which are the food capture webs of the host, many *Argyroides* were found in the eggsac webs of *Aranea crassa* (Walck.) while the maternal spider was standing on the eggsac. Eggsac webs are non-sticky arrays of silk (ca. 5x5x9 cm) which surround the eggsac. Up to 15 juvenile *Argyroides* (body length: 1.0-2.5 mm) were found motionless in a single eggsac web.

Of 95 *Argyroides* (11 males, 12 females, and 72 juveniles) found during summer, 85% were associated with *Aranea* webs (Table 2). All adults were found on orb webs.

The casual survey ($n = \text{ca. } 50$ spiders) conducted to reveal population structure of *Argyroides* in early spring revealed the presence of three adults (2 males, 1 female), numerous sub-adult males (ca. 20), and juveniles (ca. 30).

Locomotion on webs.—*Argyroides* stuck to the cribellate webs of *Badumna*. After landing on the web, *Argyroides* “froze”, then carefully tried to remove any legs stuck to the silk. If successful, the spider proceeded to clean the freed leg by moving the tarsi through its chelicerae. Often, however, *Argyroides* had great difficulty in freeing legs and remained motionless on the web, for several minutes at a time, in a posture not normally associated with resting. If the spider was unable to free itself completely after ca. 10 min, I removed it manually and returned it to its own web. In contrast, *Argyroides* was seen to walk through large glue droplets on non-cribellate sticky webs of *Aranea* without any apparent difficulty. *Argyroides* also had no evident difficulty moving on the non-cribellate sticky webs of *Achaearanea*.

Mortality on webs.—*Argyroides* varied greatly in its ability to survive on the host's web. Of the 6 *Argyroides* placed on webs of *Badumna*, 5 were killed in 42 spider-days; of the 5 *Argyroides* placed on webs of *Achaearanea*, 3 were killed in 51 spider-days; and 6 *Argyroides* placed on webs of *Aranea*, none were killed in 81 spider-days although one died of natural causes (that is, it was found dead rather than eaten). *Argyroides* survived significantly better on webs of *Aranea* compared with webs of *Badumna* ($Z = 2.10$, $P < 0.05$), and survival on webs of *Achaearanea* was intermediate to, and not significantly different from survival on webs of either of the other species (*Aranea* versus *Achaearanea*: $Z = 1.68$ $P < 0.1$; *Achaearanea* versus *Badumna*: $Z = 0.85$, $P < 0.1$).

Capture efficiencies.—*Argyroides* varied significantly in its ability to capture food on the three types of host webs, being successful in capturing food in webs of *Aranea* in 81% of the trials ($n = 22$), successful in 44% of the trials on webs of *Achaearanea* ($n = 18$), and successful in only 6% of the trials on webs of *Badumna* ($n = 17$) ($P < 0.001$, $\chi^2 = 21.42$, 2 *df*).

Foraging behavior.—*Argyroides* obtained food by either feeding with the host, stealing the host's food bundles, or capturing *Drosophila* caught on the host's web. For all these methods of food capture, *Argyroides* proceeded through the following six steps: (1) *Argyroides* stands in its cryptic posture, not responding to food; (2) *Argyroides* stands in its alert posture; (3) *Argyroides* moves on web but not apparently towards a food item; (4) *Argyroides* moves towards a food item; (5) *Argyroides* touches the food; (6) *Argyroides* feeds. The “cryptic” and “alert”

Table 1.—Webs occupied during winter by juvenile *Argyroides* ($n = 133$) expressed as percentages of the total number of *Argyroides* found.

| Host | Description of host's web | Condition of host's web | Position of <i>Argyroides</i> ' web | Percentage of <i>Argyroides</i> found |
|--|---|----------------------------------|--|---------------------------------------|
| <i>Argyroides pustulosa</i> (Araneidae) | Non-cribellate sticky orb | Maintained & used by host | Attached to host's web | 47.4% |
| <i>Aranea crassa</i> (Araneidae) | Eggcase lattice | Maintained & used by host | Attached to host's web | 12% |
| <i>Leucauge dromedaria</i> (Araneidae) | Non-cribellate horizontal orb surrounded by a maze of threads | Maintained & used by host | Attached to host's web | 0.8% |
| <i>Cyclosa trilobata</i> (Araneidae) | Non-cribellate vertical orb with stabilimentum | Maintained & used by host | Attached to host's web | 0.8% |
| <i>Argyroides antipodiana</i> (Theridiidae) | | | In isolation | 7.5% |
| | | | Isolated but behind old, unidentified silk | 6.0% |
| | | | | (13.5%) |
| <i>Achaearanea</i> sp. (Theridiidae) | Non-cribellate sticky space web | Maintained & used by host | Attached to host's web | 6.0% |
| <i>Cambridgea</i> sp. (Agelenidae) | Non-cribellate non-sticky large sheet web (<100 cm ²) | Maintained & used by host | Attached to host's web | 6.6% |
| <i>Stiphidion</i> sp. (Agelenidae) | Non-cribellate non-sticky small sheet web (<10 cm ²) | Maintained & used by host | Attached to host's web | 1.5% |
| <i>Pholcus</i> sp. (Pholcidae) | Non-cribellate non-sticky space web | Maintained & used by host | Attached to host's web | 0.8% |
| <i>Badumna longinquus</i> (Amaurobiidae) | Cribellate space web | Maintained & used by host | Attached to host's web | 0.8% |
| | | Maintained & used by host | Isolated but behind host's web | 6.0% |
| | | In disrepair & abandoned by host | Attached to host's web | 3.8% |
| | | | | (10.6%) |

postures are described elsewhere (Whitehouse 1986). The closest step towards feeding reached by the *Argyroides* during the observation period was recorded.

In nearly all the tests on webs of *Aranea*, *Argyroides* reached step 6 (Fig. 1). *Argyroides* on the webs of *Achaearanea* either stopped at step 3 or continued until it obtained food (step 6); it rarely failed to obtain food once it had located it (Fig. 1). *Argyroides* often made several attempts to obtain food on the webs of both *Achaearanea* and *Aranea* before succeeding. *Argyroides* on the web of *Badumna* rarely passed step 3.

Table 2.—Webs occupied during summer by *Argyroides* ($n = 95$: 23 adults, 72 juveniles) expressed as percentages of the total number of *Argyroides* found. Adults were only found on *Aranea pustulosa* webs.

| Host | Description of host's web | Condition of host's web | Position of <i>Argyroides</i> ' web | Percentage of <i>Argyroides</i> found |
|--|---|----------------------------------|--|---------------------------------------|
| <i>Aranea pustulosa</i> (Araneidae) | Non-cribellate sticky orb | Maintained & used by host | Attached to host's web | 82.1% |
| | | In disrepair & abandoned by host | Attached to host's web | 3.2% |
| | | | | (85.3%) |
| <i>Aranea crassa</i> (Araneidae) | Eggcase lattice | Maintained & used by host | Attached to host's web | 12% |
| <i>Cambridgea</i> sp. (Agelenidae) | Non-cribellate non-sticky large sheet web (<100 cm ²) | Maintained & used by host | Attached to host's web | 3.2% |
| <i>Stiphidion</i> sp. (Stiphidiinae) | Non-cribellate non-sticky large sheet web (<10 cm ²) | Maintained & used by host | Attached to host's web | 1.0% |
| <i>Argyroides antipodiana</i> (Theridiidae) | | | In isolation | 5.3% |
| | | | Isolated but behind old, unidentified silk | 4.2% |
| | | | | (9.5%) |
| Unidentified | Unidentified | In disrepair & abandoned by host | No web present | 1.0% |

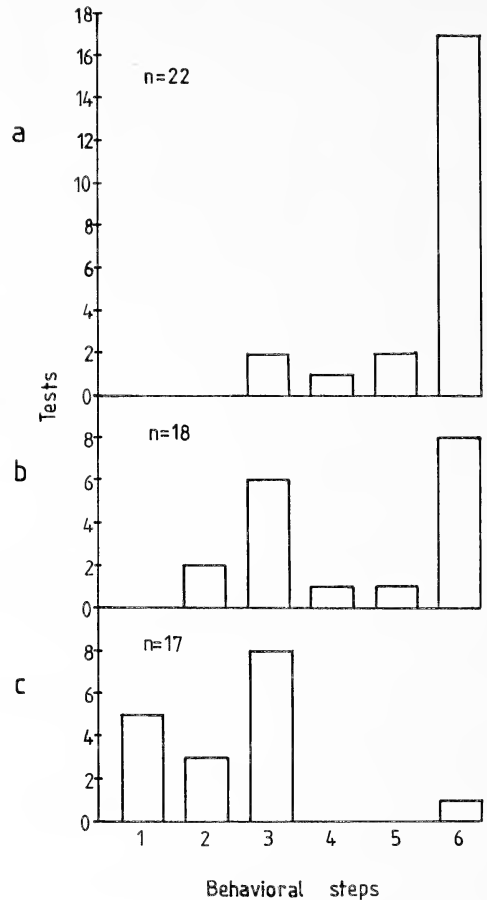
DISCUSSION

Field surveys of hosts of *Argyroides*.—*Argyroides* were found to mainly kleptoparasitize the webs of a single host species, *Aranea*. This characteristic supports the conclusion gained from its wide range of foraging behaviors (Whitehouse 1986) that *Argyroides antipodiana* is a specialist kleptoparasite.

The field surveys also reveal that the population structure of *Argyroides* appears to be seasonal. *Argyroides* overwinter as juveniles, mature in spring, and reproduce in summer. More work is needed to determine if one generation survives for the whole year or if there are two generations, a short one which survives only through summer and a longer one which overwinters.

Evidently *Argyroides* was more restricted to webs of *Aranea* during the summer than during winter. This may be linked to the seasonal variation in population structure. Adult *Argyroides*, which only exploited *Aranea*, were abundant in summer, scarce in spring, and absent in winter. The feeding and mortality experiments showed that *Argyroides* was significantly better at obtaining food and surviving on the webs of *Aranea* than on any other webs. Thus adults which must reproduce within a short period of time (probably ca. one month) in summer, are apparently limited to the webs of *Aranea* from which they can obtain food. Juvenile *Argyroides* are able to survive for a long time in the laboratory (three months) without feeding (unpubl. data). While they are overwintering they need a web for shelter only, and so would not be restricted to the webs of *Aranea*. In

Fig. 1.—Distribution of the final behavioral step (as defined in foraging behavior section of results) that *Argyroides* reached during a feeding bout: a, *Argyroides* on the webs of *Aranea*; b, *Argyroides* on the webs of *Achaearanea*; c, *Argyroides* on the webs of *Badumna*.



spring, when they need food to grow and mature, they apparently move to the webs of *Aranea*.

Steps towards obtaining food.—The sequence of behaviors leading towards food acquisition was arrested for many spiders at step 3 (Fig. 1). In particular, nearly all spiders on the webs of *Badumna* and half on the webs of *Achaearanea* stopped at this point. Spiders that proceeded past step 3 (moving on the web) usually persevered and continued to approach food items until they managed to obtain one. This observation suggests that *Argyroides* may be better at obtaining food on webs of *Aranea* because it is unable to interpret vibrations on the webs of *Badumna* and, to some extent, *Achaearanea*. That is, *Argyroides* appears capable of sensing vibrations upon the webs of *Badumna* and *Achaearanea* (in that it responds to the vibrations by moving), but is apparently unable to determine the direction from which the vibrations are coming. A complicating factor on the web of *Badumna*, however, is that *Argyroides* is unable to walk on these webs. Nevertheless, *Argyroides* uses its own web as a scaffolding to approach food on a hosts' web (Whitehouse 1986) and so could conceivably use this to approach food on the web of *Badumna* and thus avoid, to a large extent, walking on the web of this host.

Host preference.—The ability of *Argyroides* to inhabit the webs of *Badumna* (cribellate, sticky, space web), *Achaearanea* (non-cribellate, sticky vertical orb

web) was examined by looking at three parameters: the abilities to move, survive, and feed on the host's web. *Argyrodes* was able to walk on webs of both *Aranea* and *Achaearanea*, but they became ensnared by the cribellate glue on webs of *Badumna*. In both ability to survive and feed, *Argyrodes* performed best on webs of *Aranea*, worst on webs of *Badumna*, and intermediately on webs of *Achaearanea*. Thus these parameters are probably major factors limiting adult *Argyrodes* to the webs of *Aranea* in the field. It is interesting, however, that other non-cribellate sticky orb webs, such as those of *Cyclosa trilobata* (Urqu.) which, common along with *Aranea* in the habitat of *Argyrodes antipodiana*, were not exploited. Thus not all orb webs and their residents fulfill the criteria upon which *Argyrodes antipodiana* bases its choice of hosts.

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XENONEMESIA, UN NUEVO GENERO DE NEMESIIDAE (ARANEAE, MYGALOMORPHAE)

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ABSTRACT

Xenonemesia platense, a new genus and species of nemesiid spider from Argentina and Uruguay, is described and figured. The new genus is characterized by having a wide sternum, slightly raised tarsal organ, slight scopula, apical article of posterior spinnerets domed, and by the absence of serrula, male tibial apophyses, keels on the bulb, and third claw.

EXTRACTO

Se describe e ilustra a *Xenonemesia platense*, un nuevo género y especie de Argentina y Uruguay. El nuevo género se caracteriza por tener esternón ancho, órgano tarsal ligeramente elevado, escópula rala, artejo apical de las hileras posteriores hemisférico, y por la ausencia de sérrula, apófisis tibiales en el macho, carenas en el bulbo y tercer uña.

INTRODUCCION

Todos los géneros de Nemesiidae descritos de Sudamérica, excepto *Spelocteniza* Gertsch (Nemesiidae cavernícola *incertae sedis*) y *Acanthogonatus* Karsch (Anaminae), pertenecen a las subfamilias Pycnothelinae y Diplothelopsinae (Raven 1985). El descubrimiento de una nueva especie de Argentina y Uruguay que no pertenece a ninguno de estos grupos, ni puede tampoco ser ubicada en ninguno de los grupos de Nemesiidae reconocidos por Raven (1985) lleva a describir un nuevo género.

MATERIALES Y METODOS

Las medidas están dadas en milímetros. La notación de la dentición de uñas, quetotaxia y tricobotriotaxia se hace según Goloboff y Platnick (1987). Otras abreviaturas utilizadas son las usuales, y se pueden encontrar en Galiano (1970). Siguiendo a Coyle (1974) se denomina cerda ensiforme a aquella que tiene su extremo romo, y atenuada a aquella que se adelgaza gradualmente. El material estudiado está depositado en las siguientes instituciones: Facultad de Ciencias Exactas y Naturales de la Universidad de Buenos Aires (FCEN), a cargo del Dr. Juan C. Giacchi; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), a cargo del Dr. Emilio A. Maury; American Museum of Natural History (AMNH), a cargo del Dr. Norman I. Platnick.

Xenonemesia, nuevo género

Especie tipo.—*Xenonemesia platense*, n. sp.

Etimología.—El nombre genérico, derivado de *Nemesia* (género tipo de la familia) y la palabra griega xeno (extraño), se refiere a que el nuevo género no parece estar emparentado cercanamente con ninguno de los de la familia Nemesiidae previamente descriptos. Es de género femenino.

Diagnosis.—Se diferencia de los demás géneros conocidos de la familia por presentar simultáneamente esternón ancho, cymbium sin cerdas engrosadas, bulbo sin carenas, tibia I del macho sin apófisis, escópula tarsal poco densa en tarsos anteriores y ausente en los posteriores, uña tarsal inferior ausente y artejo apical de las hileras posteriores hemisférico.

Los demás géneros de Nemesiidae de Argentina o Uruguay se diferencian fácilmente de *Xenonemesia* por tener escópula tarsal y metatarsal densa en patas anteriores (y casi siempre, escópula en tarsos III).

Descripción.—Ver descripción de la especie tipo.

Xenonemesia platense, nueva especie

Figs. 1-14

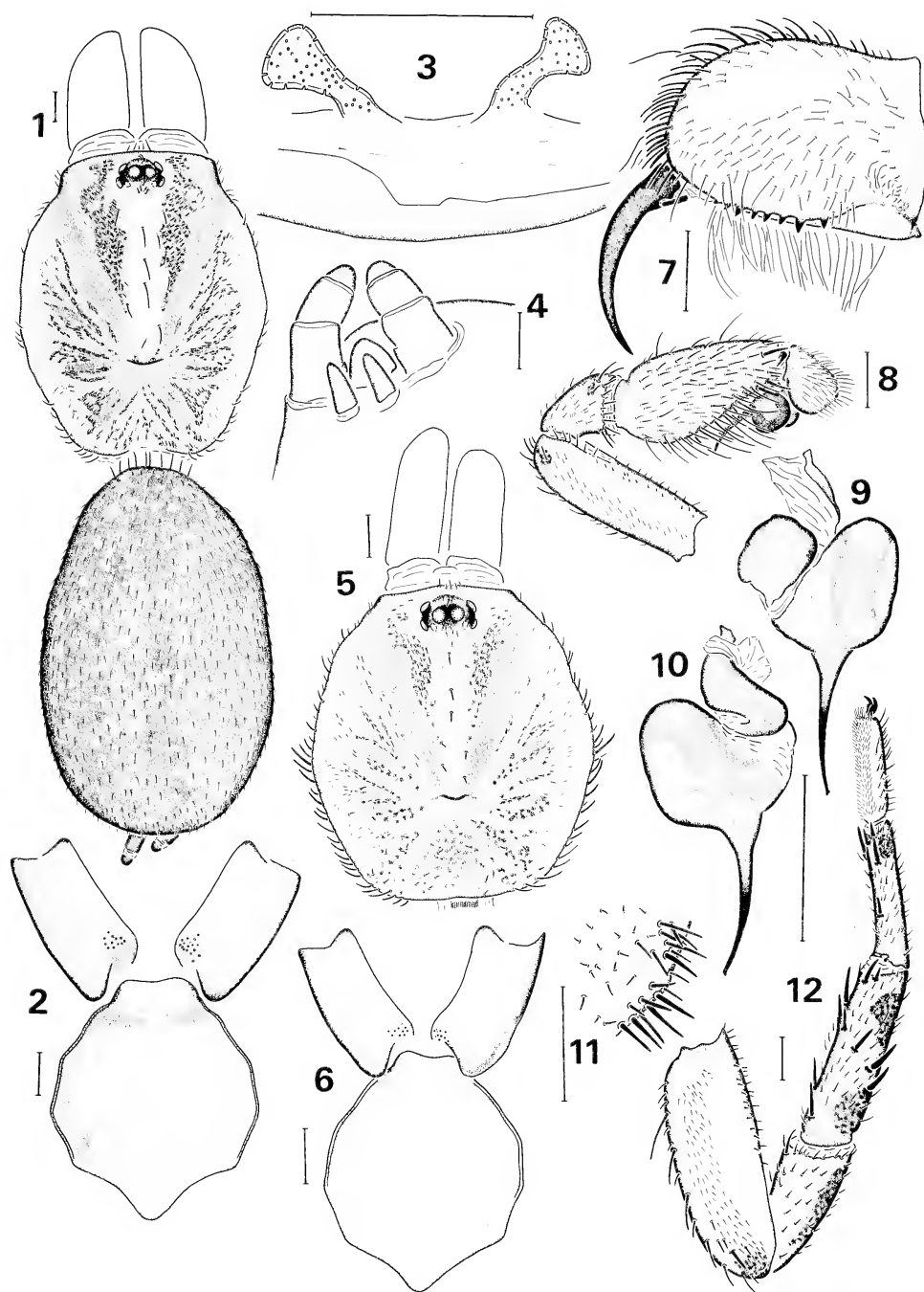
Tipos.—Holotypus hembra de Argentina, provincia de Buenos Aires: General Pacheco, 27 IX 1980 (P. Goloboff), MACN 8603. Los siguientes paratypi: Argentina, provincia de Entre Ríos: Ao. Gualeacán, 5-6 II 1983 (P. Goloboff), 3 machos, 4 hembras (MACN 8608, 8609); Parque Nacional El Palmar, 18 IV 1981 (P. Goloboff, A. Zanetic), 1 hembra (AMNH).

Etimología.—El nombre específico se refiere a la distribución de la especie, que comprende Argentina y Uruguay, países que hasta principios del siglo pasado formaron parte del virreinato del Río de la Plata.

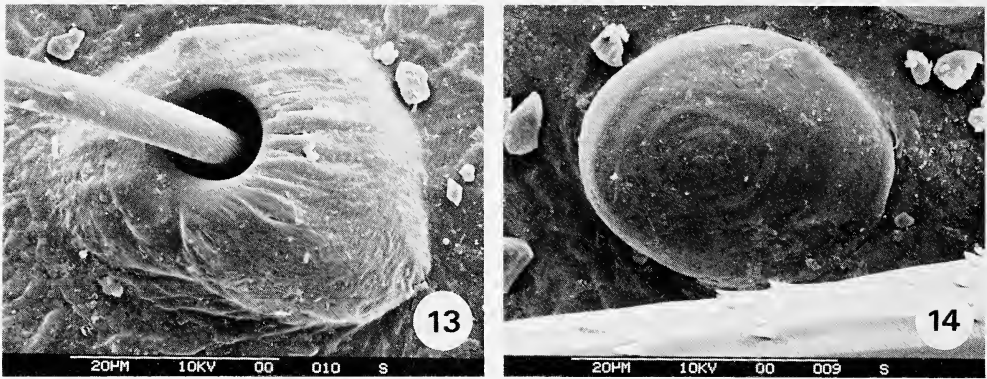
Diagnosis.—Se reconoce fácilmente por los caracteres genéricos y por su colorido, con tres fajas claras en el cefalotórax y el abdomen sin "chevron" (Figs. 1, 5).

Descripción de la hembra holotypus.—Largo total, 15.85. Cefalotórax (Fig. 1) de largo 5.66, ancho 4.53; RC convexa; RT más baja y declive hacia atrás; ancho 0.80 del largo. RC de ancho 0.77 de su largo; largo 0.70 del largo del cefalotórax; ancho 0.86 del ancho de la RT. Fóvea ligeramente procurva; ocupa 0.15 del ancho de la RT. Tubérculo ocular elevado, ocupa 0.30 del ancho de la RC. OMA ligeramente mayores que los OMP; OLA ligeramente mayores que los OLP. En el tubérculo ocular, 3 cerdas gruesas y 8 más pequeñas por delante de los OMA; 10 cerdas por detrás de los OMA. En el clípeo, 7 cerdas dirigidas hacia adelante. Por detrás del tubérculo ocular, una fila media de 3 cerdas gruesas y largas y dos filas laterales de unas 5 cerdas más pequeñas.

Quelíceros con rastrillo débil, formado por cerdas gruesas atenuadas; margen externo inerme, interno con 7 dientes que decrecen en tamaño hacia el ápice; parte basal del canal con 9 dentículos; cara anterior sin pelos clavados; gancho no aserrado y sin carenas. Coxas de los palpos con 12 a 17 espínulas, sin sérrula. Labio inerme, de largo 0.48 del ancho. Esternón (Fig. 2) con su margen ligeramente rebordeado, de ancho 0.95 del largo, revestido de cerdas duras (sobre todo en el margen); sigillas pequeñas, ovales, submarginales.



Figs. 1-12.—*Xenonemesia platense*: 1-4, Hembra; 5-12, Macho; 1, cefalotórax y abdomen; 2, 6, esternón, labio y coxas de los palpos; 3, espermatecas, ventral; 4, hileras, ventrolateral; 5, cefalotórax; 7, quelícero derecho, cara anterior; 8, palpo izquierdo, prolateral; 9-10, bulbo derecho, caras opuestas; 11, detalle del margen del esternón (con sigilla III); 12, pata I derecha, prolateral; (1-2, Holotypus 8603 MACN; 3, 8602 MACN; 4, 8601 MACN; 5-6, 11, 8604 MACN; 7-10, 12, Paratypus 8608 MACN.). Escala = 0.5 mm.



Figs. 13-14.—*Xenonemesia platense*, hembra AMNH: 13, tricobotria del tarso IV; 14, órgano tarsal del tarso IV.

Pata I distinta de la II, más gruesa, inerme, con sus uñas más cortas y gruesas; metatarso cónico, adelgazado hacia del extremo distal. Escópula muy rala en tarso I, más rala aún en tarso II y tercio apical de metatarso I, ausente en tarsos III y IV y metatarsos II-IV. Todas las patas sin peines metatarsales. Organo tarsal ligeramente elevado y convexo (Fig. 14). Cutícula de las patas lisa (Figs. 13, 14). Tarsos I-IV íntegros.

Medidas de las patas:

| | Fémur | Patella | Tibia | Metatarso | Tarso | Total |
|-------|-------|---------|-------|-----------|-------|-------|
| I | 3.53 | 2.53 | 2.53 | 1.50 | 1.03 | 11.12 |
| II | 3.00 | 2.00 | 1.93 | 1.37 | 1.20 | 9.50 |
| III | 2.60 | 1.40 | 1.67 | 1.90 | 1.33 | 8.90 |
| IV | 3.63 | 2.13 | 2.73 | 3.06 | 1.47 | 13.02 |
| Palpo | 2.20 | 1.27 | 1.43 | — | 1.13 | 6.03 |

Uñas tarsales superiores: pata I, ambas uñas, T-T ext., t int.; II, ambas uñas con dos filas de T-T-T; III y IV, ambas uñas con T-T-T-T ext., T-T-T int.; palpo, T-T-T en promargen. Uña inferior ausente en todas las patas. Tricobotrias: Tibias I-IV con dos filas de 5 a 6 en la 1:2 B a 3:4 B; tibia del palpo, fila ant. 6 (1:1), post. 7 (1:1). Metatarsos con una fila diagonal y un grupo de 3 o 4 en el ápice; I, 12 (2:3 A); II, 11 (2:3 A); III, 10 (3:4 A); IV, 12 (3:4 A). Tarsos con una fila en zig-zag en los 3:4 A; tarso I, 10; II-IV, 12; palpo, 9 (2:3 A). Botria ligeramente corrugados (Fig. 13). Quetotaxia: Fémures inermes. Patella III, 1-1-1 P, 1 r; IV, 1 r; I, II y palpo, inermes. Tibia II, 1 p sup (1:3 a), 1 v ant a; III, 1-1 P (2:3 B), 1 D A, 3 V A; IV, 1-1/0-1 R, 0-2/1-2 V A; palpo, 2 V ANT A; I, inerme. Metatarso II, 1-0-1 D POST, 1-1 V POST (2:3 A); III, 1-1-1 P, 1-1 D ANT (1:2 A), 1-0-1 D POST, 1 R A, 2-2 V (1:2 A); IV, 2-1-1-2-2/2-2-2-2 V ANT, 1-1-2 V ó 2 V A, 1-1-1/1-1 R SUP, 1-1 D ANT (1:3 A); I, inerme. Todos los tarsos inermes.

Hileras (Fig. 4): anteriores de largo 0.63, con 5 fúsculas apicales; posteriores con sus fúsculas regularmente distribuídas y de tamaño uniforme; artejo basal de largo 0.67, con 25 fúsculas (2:3 A); medio, 0.43, con 30 fúsculas; apical, 0.27, con 25 fúsculas, hemisférico. Spermatecas como en la Fig. 3.

Todo el cuerpo revestido con cerdas delgadas, atenuadas, y pelos en forma de bastón, muy pequeños y de color claro, acostados. Borde anterior del abdomen

con cerdas engrosadas parecidas a las de *Migas vellardi* (Goloboff y Platnick, 1987, fig. 7), pero dirigidas hacia afuera y más largas y rectas.

Cefalotórax marrón rojizo oscuro, con 3 bandas longitudinales más claras bien nítidas. Patas de color marrón, con manchas oscuras en ápice de fémures, tibias y metatarsos y en patellas. Abdomen oscuro, sin "chevron", con manchitas blancas más numerosas a los lados del área cardíaca (Fig. 1). Vientre de color claro con manchas oscuras.

Descripción del macho paratypus 8608 MACN.—Largo total 10.20. Cefalotórax (Fig. 5) de largo 4.26, ancho 3.26, menos elevado y convexo que en la hembra; ancho 0.77 del largo. RC de ancho 0.60 de su largo; largo 0.42 del largo del cefalotórax; ancho 0.51 del ancho de la RT. La fóvea ocupa 0.11 del ancho de la RT. Los ojos ocupan 0.38 del ancho de la RC. Por delante de los OMA, 7 cerdas; 5 en el clípeo; 5 por detrás de los OMA; una fila longitudinal de 5 por detrás del tubérculo ocular y dos filas de cerdas (más pequeñas) a los costados. Margen del cefalotórax con cerdas fuertes y gruesas.

Quelíceros con dentición y rastrillo semejantes a los de la hembra, con tumescencia interqueliceral bien evidente, pequeña, cubierta con pocas cerdas cortas (Fig. 7). Coxas de los palpos con 12 a 13 espínulas. Labio inerte, de largo 0.40 del ancho. Esternón (Fig. 6) de ancho 0.93 del largo, revestido con cerdas más gruesas que en la hembra (Fig. 11).

Pata I (Fig. 12) sin apófisis ni carenas de ningún tipo; metatarso recto, cilíndrico. Escópula muy rala (más aún que en la hembra) en tarsos I y II, ausente en tarsos III y IV y metatarsos I-IV. Tarsos I-IV íntegros.

Medidas de las patas:

| | Fémur | Patella | Tibia | Metatarso | Tarso | Total |
|-------|-------|---------|-------|-----------|-------|-------|
| I | 3.10 | 1.93 | 2.50 | 1.80 | 1.33 | 10.66 |
| II | 2.73 | 1.60 | 2.00 | 1.80 | 1.37 | 9.50 |
| III | 2.56 | 1.33 | 1.80 | 2.20 | 1.47 | 9.36 |
| IV | 3.26 | 1.73 | 2.73 | 3.33 | 1.57 | 12.62 |
| Palpo | 1.83 | 0.90 | 1.73 | — | 0.73 | 5.19 |

Uñas tarsales superiores con doble fila de dientes: pata I, ambas uñas 5 int., 6 ext.; II, ambas uñas con dos filas de 7; III, uña ant. 8 int., 9 ext., post. 10 int., 7 ext.; IV, uña ant. con dos filas de 9, post. 8 int., 7 ext. Tricobotrias: Tibias: I, II y IV, 5 ó 6 en cada fila (ocupando 2:3 a 3:4 B en la fila ant., más extendidas en la posterior); III, ant. 4 (1:2 B), post. 4 (2:3 B); palpo, ambas filas 5 (1:1). Metatarsos: I, II y III, 8 (2:3 A); IV, 11 (2:3 A). Tarsos I-IV, 8 a 10 (2:3 A); palpo, 9 (1:3 M). Quetotaxia: fémur I, 1-1-1-1-2 D; II, 1-1 D ANT (1:3 A), 1-1-1-1 D, 1-1-1 D POST; III, 1-1 D ANT (1:2 M), 1-1-1 D (1:2 B), 1-1-1 D POST (1:2 A); IV, 1-1-1 D (2:3 B); palpo, 1-1-1-1-2 D. Patella I, 1 p sup (1:3 a), 1 V A; II, 1-1/1 P SUP; III, 1-1-2 P, 1 R; IV, 1 R; palpo, 4/5 d a. Tibia I, 3 P M, 2-1-0-2-1 V, 2 V ANT A; II, 1-1 P SUP, 1-1-1-1 V (alternadas), 3 V A; III, 1-1 P, 2-1 D, 1-1 R, 2-2-3 V; IV, 1-1 P, 1 D B, 1-1 R, 2-2-3 V; palpo, 1 P A, 1 R A. Metatarso I, 1 V B, 3-2 V A; II, 1-1 P SUP, 2-2-3 V; III, 1-1-1 P, 1-1-2 D, 2-2 V, verticilo A de 5; IV, 1-1-1 P, 1-1-2 D, 2-1-2 V, verticilo A de 5. Tarsos I-IV inermes.

Palpo como en la Fig. 8; cymbium inerte, sin cerdas engrosadas; tibia con su excavación ventral poco profunda. Bulbo (Figs. 9-10) sin carenas, con el émbolo delgado. Área epigástrica con c. 35 glándulas epiándricas.

Todo el cuerpo revestido con cerdas numerosas, más cortas y gruesas que en la hembra, ensiformes, excepto en los artejos apicales de patas y palpos, que tienen cerdas atenuadas.

Colorido semejante al de la hembra.

Variaciones.—No se observaron variaciones de importancia en los caracteres mencionados, excepto en la forma de la fóvea: algunos ejemplares presentan la fóvea con sus bordes ligeramente recurvados (como el macho 8604 MACN, Fig. 5).

En uno de los machos de General Pacheco hay sólo 1-1 V, 1-1 P, 1 V ANT en tibia I; en los demás machos examinados la quetotaxia es similar a la del paratypus 8608 MACN.

Historia natural.—En el Parque Nacional El Palmar *Xenonemesia platense* fue colectada en la barranca del río Uruguay, bajo piedras, en un ambiente húmedo y sombrío, junto con *Grammostola* sp., *Homoeomma uruguayensis* (Mello-Leitão, 1946), *Stenoterommata argentinensis* (Schiapelli y Gerschman de Pikelin, 1958), *Stenoterommata* sp., *Actinopus* sp. e *Idiops clarus* (Mello-Leitão, 1946). En el arroyo Gualayán, en lugar llano, se la encontró en un monte más abierto y xerófilo (donde abundan plantas como *Opuntia* y *Aspidosperma*), en los montículos de tierra al pie de árboles. Otras Mygalomorphae colectadas en este lugar fueron *Grammostola* sp. (distinta de la de P. N. El Palmar), *Eupalaestrus campestratus* (Simon, 1897), *Stenoterommata* sp., *Actinopus* sp. e *Idiops clarus*. En General Pacheco, en un ambiente alterado, *Xenonemesia platense* fue encontrada en los montículos de tierra al costado de los caminos en un parque con suaves barrancas, donde no se encontraron otras Mygalomorphae.

Los ejemplares fueron hallados en cuevas poco profundas (menos de 10 cm de profundidad), sin opérculo, de recorrido bastante irregular, de 1 cm de ancho aproximadamente, con sus paredes cubiertas con muy poca seda; habitualmente cierran la cueva durante el día amontonando tierra y seda en la entrada. Un ejemplar colectado con la ooteca estaba en una cámara oval, de 20 o 25 mm de largo y 10 o 15 de ancho, cerrada, con el resto de la cueva tapado.

Se observó que ejemplares en cautiverio pueden capturar sus presas sin tener cueva construida. Mientras comen la presa, depositan seda en el sustrato, con movimientos circulares similares a los de Theraphosidae (Eberhard 1967).

Material examinado.—**ARGENTINA:** BUENOS AIRES; Buenos Aires, 1979 (D. Martínez), 1 hembra, 1 macho jov. (FCEN), General Pacheco, 28 X 1979 (P. Goloboff), 2 hembras (MACN 8601), 5 I 1980 (P. Goloboff), 3 hembras (MACN 8602), 27 IX 1980 (P. Goloboff), 2 machos, 1 hembra (MACN 8604), 18 X 1980 (P. Goloboff), 1 hembra (MACN 8605). ENTRE RÍOS; Parque Nac. El Palmar, 12-16 II 1980 (P. Goloboff), 3 hembras, 2 machos jov. (MACN 8606), 18 IV 1981 (P. Goloboff, A. Zanetic), 1 macho jov. (MACN 8607), Arroyo Gualayán, 5-6 II 1983 (P. Goloboff), 2 machos jov., 1 hembra jov. (MACN 8618), 13 X 1984 (P. Goloboff, C. Szumik), 2 hembras, 1 macho jov., 1 hembra jov. (MACN 8610), 27 IX 1987 (P. Goloboff, C. Szumik), 1 macho, 1 hembra, 2 jows. (MACN 8619). **URUGUAY:** LAVALLEJA; Picada de Rodríguez, 8 VII 1957 (sin colector), 1 macho joven (MACN 8611), bajo piedra. **COLONIA;** San Juan, XII 1950 (R. Ringuelet), 1 macho jov. (MACN 8612).

RELACIONES DE *XENONEMESIA* CON OTRAS NEMESIIDAE

Las únicas sinapomorfías de la familia Nemesiidae son las uñas tarsales superiores anchas y con dientes biseriados y la uña del palpo de la hembra con dientes en promargen; dichos caracteres sostienen la inclusión de *Xenonemesia* en

Nemesiidae, al menos mientras no se acepte la hipótesis alternativa de que son una sinapomorfía de Crassitarsae (Theraphosoidina mas Nemesiidae) y no sólo de Nemesiidae (Raven 1985:28).

Las interrelaciones de las Nemesiidae son un poco inciertas; el cladograma que Raven (1985, fig. 4) ha presentado tiene un gran número de homoplasias, como ya fue destacado por su mismo autor (1985:46). El descubrimiento de *Xenonemesia* complica aún más el panorama, porque este género comparte algunos caracteres derivados con algunos grupos de Nemesiidae y otros caracteres con otros grupos. La uña tarsal inferior falta sólo en Diplothelopsinae y algunas *Acanthogonatus* y Pycnothelinae. El esternón es ancho en algunas Bemmerinae y Diplothelopsinae (no en todas, como cita Raven 1985:97). El artejo apical de las hileras laterales posteriores es hemisférico en Nemesiinae y algunas Ixamatinae, Pycnothelinae, Bemmerinae y *Acanthogonatus*. La sérrula falta también en Nemesiinae y algunas Ixamatinae, Pycnothelinae y Anaminae.

Dado que según los caracteres mencionados la inclusión de *Xenonemesia* en cualquiera de estos grupos requiere un grado de homoplasia más o menos similar, sus relaciones con las demás Nemesiidae permanecen inciertas por ahora.

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El Dr. Norman I. Platnick, con la gentileza habitual en él, tomó las fotomicrografías que ilustran este trabajo y, al igual que el Dr. Robert J. Raven (Queensland Museum, Australia) y Prof. María E. Galiano (MACN), hizo la lectura crítica del manuscrito.

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***TYPHLOCHACTAS MITCHELLI*, A NEW SPECIES OF
EYELESS, MONTANE FOREST LITTER SCORPION FROM
NORTHEASTERN OAXACA, MEXICO
(CHACTIDAE, SUPERSTITIONINAE, TYPHLOCHACTINI)**

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ABSTRACT

Typhlochactas mitchelli, new species, is described from Cerro Ocote, near Tenango, Oaxaca, Mexico. This is the second species of *Typhlochactas* discovered in montane forest litter. Based on its cheliceral dentition, *T. mitchelli* is most closely related to the other forest litter species, *T. sylvestris* Mitchell & Peck, also from Oaxaca.

INTRODUCTION

The first eyeless scorpion from montane forest litter was discovered along the east slopes of the outer range of the Sistema Montañoso Poblano Oaxaqueño near Valle Nacional, Oaxaca by Dr. Stewart B. Peck in May of 1971 (Mitchell and Peck 1977). This discovery was highly significant because it was the first species of the genus *Typhlochactas* (all of which are eyeless, depigmented scorpions) collected outside the cave environment. *Typhlochactas* now consists of four species: *T. rhodesi* Mitchell from La Cueva de la Mina in Tamaulipas; *T. reddelli* Mitchell from La Cueva del Ojo de Agua de Tililapan in Veracruz; *T. sylvestris* Mitchell and Peck from montane forest litter in Oaxaca; and *T. cavicola* Francke from La Cueva del Vandalismo in Tamaulipas (Mitchell 1968; Mitchell and Peck 1977; Francke 1986). A fifth species, *T. elliotti* Mitchell from El Sotano de Yerbaniz in San Luis Potosí, has been transferred to a separate genus, *Sotanochactas* (Mitchell 1971; Francke 1986).

It is the purpose here to describe another species of this remarkable genus, the second one from montane forest litter. It is most closely related to *T. sylvestris*, the other forest litter species, but differs from it in a number of significant features. The new species was collected on Cerro Ocote near Tenango, Oaxaca along the northeastern edge of the Sistema Montañoso Poblano Oaxaqueño.

***Typhlochactas mitchelli*, new species**
Figs. 1-14

Type data.—Holotype male, paratype male, and subadult paratype female taken from Cerro Ocote, 5 mi S Tenango, Oaxaca, México in April 1987 (A.

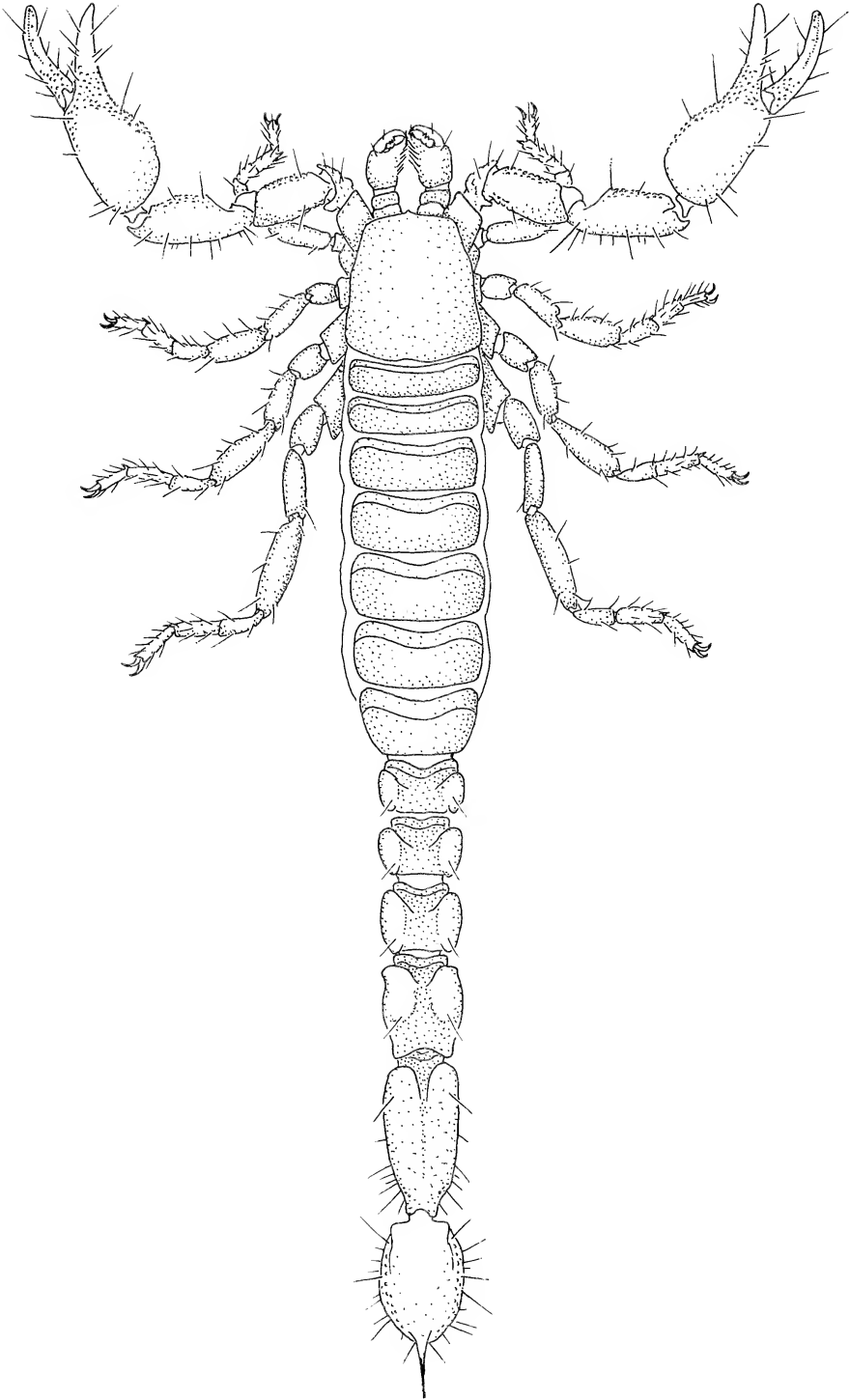
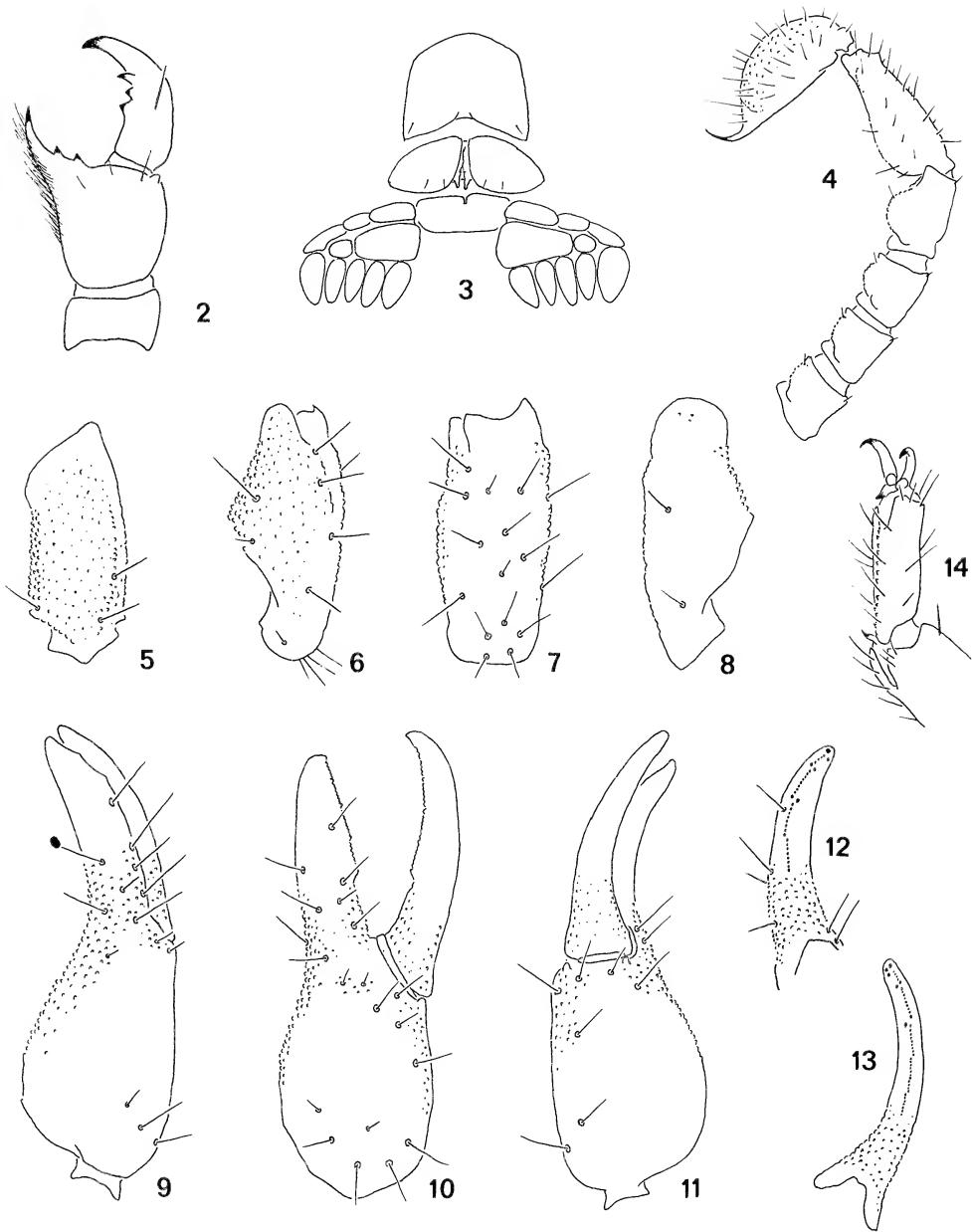


Fig. 1.—Dorsal view of holotype male of *Typhlochactas mitchelli*, new species.



Figs. 2-14.—External morphology of holotype male of *Typhlochactas mitchelli*, new species: 2, dorsal aspect of right chelicera; 3, ventral aspect of sternum, genital operculi, and pectines; 4, lateral aspect of metasoma and telson; 5, dorsal aspect of pedipalp femur; 6, dorsal aspect of pedipalp tibia; 7, external aspect of pedipalp tibia; 8, ventral aspect of pedipalp tibia; 9, dorsal aspect of pedipalp chela; 10, external aspect of pedipalp chela; 11, ventral aspect of pedipalp chela; 12, inner margin of pedipalp chela fixed finger, showing placement of trichobothria and dentition; 13, inner margin of pedipalp chela movable finger, showing dentition; 14, retrolateral aspect of tarsomere II of left leg IV.

Grubbs, A. Cressler, P. Smith). Holotype male, paratype male, and paratype subadult female deposited in the American Museum of Natural History, New York.

Etymology.—The specific epithet is a patronym honoring Dr. Robert W. Mitchell of Texas Tech University, who inspired my initial interest in arachnids, for his contributions to Mexican scorpiology and biospeleology.

Distribution.—Known only from the type locality.

Diagnosis.—Adult males 8.49-8.99 mm long. Eyeless. Color pale yellow brown, except for posterior mesosomal segments and metasoma, which are light orange brown. Carapace, tergites, and metasoma sparsely to moderately finely granular; pedipalps more coarsely granular. Metasomal segment V slightly longer than carapace and about 1.85 times longer than wide. Cheliceral fixed finger with only three teeth; basal and medial teeth not combined into a compound tooth. Movable finger with four teeth: distal internal, distal external, medial, and basal. Pedipalps: trichobothrial pattern typical of genus (Mitchell and Peck 1977); chela relatively robust with palm length/width ratio 1.71-1.73; chela fingers shorter than carapace; fixed finger of chela with four slightly oblique rows of granules on dentate margin, restricted to distal two-thirds of finger; movable finger with five such rows. Legs armed with prolateral pedal spurs; ventral aspect of tarsomere II with median row of minute spinules flanked by three to four pairs of relatively stout setae.

Description.—Based on adult males; measurements of these two males are given in Table 1.

Coloration: Prosoma and first six mesosomal segments pale yellow brown; mesosomal segment VII (tergite and sternite) slightly darker than preceding segments. Pectines whitish. Metasoma uniformly light orange brown. Telson pale yellow brown; aculeus orange brown. Chelicerae and legs pale yellow. Pedipalps uniformly pale yellow brown, slightly darker than body.

Prosoma: Carapace (Fig. 1) subquadrate; length slightly greater than posterior width. Weakly sclerotized; surface sparsely, finely granular with a few small setae. Anterior margin weakly convex, with very subtle median projection. Median longitudinal furrow essentially obsolete. Median and lateral eyes absent; ocular tubercle absent. Sternum smooth, subquadrate; anterior margin gently convex, posterior margin concave, lateral margins diverging distally; small posteromedial depression present.

Mesosoma: Tergites I-VII weakly sclerotized, acarinate; pre-tergites smooth; post-tergites moderately finely granular. Genital operculum (Fig. 3) subelliptical, completely divided longitudinally; genital papillae well developed. Pectines (Fig. 3): more or less unsclerotized, with three marginal lamellae, two middle lamellae, and five pectinal teeth. Proximal middle lamella much larger than second. Pectinal lamellae and basal portion of teeth moderately covered with fine whitish microchaetes; distal third of pectinal teeth with conspicuous, dense, peg sensillae. Sternites III-VII smooth, sparsely setose; stigmata small, circular.

Metasoma (Fig. 4): Segments I-III wider than long; V 1.82-1.85 times longer than wide. Segments I-IV: Dorsolateral carinae on I-IV very faint, indicated by a few small distal granules; other carinae obsolete. Dorsal and lateral surfaces with moderately dense, fine granulation; ventral surfaces smooth to sparsely, finely granular; setation of first four segments sparse. Segment V: distinctly longer than carapace; dorsolateral carinae faint, granular throughout; other carinae obsolete.

Table 1.—Measurements in mm and pectinal tooth counts of the holotype and paratype males of *Typhlochactas mitchelli*, n. sp.

| | Holotype Male | Paratype Male |
|----------------------------|----------------|----------------|
| Total length | 8.99 | 8.49 |
| Carapace length | 1.17 | 1.14 |
| Mesosoma length | 2.66 | 2.43 |
| Metasoma length | 3.61 | 3.46 |
| length/width I | 0.45/0.73 | 0.45/0.74 |
| length/width II | 0.52/0.68 | 0.50/0.67 |
| length/width III | 0.55/0.69 | 0.55/0.67 |
| length/width IV | 0.80/0.71 | 0.72/0.65 |
| length/width V | 1.29/0.71 | 1.24/0.67 |
| Telson length | 1.55 | 1.46 |
| Vesicle length/width/depth | 1.17/0.73/0.59 | 1.05/0.70/0.55 |
| Aculeus length | 0.38 | 0.41 |
| Pedipalp length | 3.43 | 3.27 |
| Femur length/width | 0.85/0.35 | 0.82/0.33 |
| Tibia length/width | 0.98/0.39 | 0.90/0.38 |
| Chela length/width/depth | 1.60/0.52/0.55 | 1.55/0.51/0.55 |
| Palm length | 0.90 | 0.87 |
| Fixed finger length | 0.70 | 0.68 |
| Movable finger length | 0.92 | 0.90 |
| Pectinal tooth count | 5-5 | 5-5 |

Setation moderate, with most setae on ventral aspect. All surfaces with moderately dense, fine granulation. Dorsal surface with narrow median longitudinal furrow anteriorly and rounded, shallow depression posteriorly. Sum of metasomal I-V lengths 3.04-3.09 times greater than carapace length.

Telson (Fig. 4): Vesicle flattened dorsally, moderately globose ventrally; telson as wide as first metasomal segment, wider than segments II-V. Lateral and ventral aspects of vesicle with moderately dense, fine granulation; about 20 pairs of setae. Aculeus very slender and strongly curved.

Chelicerae: Fixed finger (Fig. 2) with only three individual teeth (distal, median, and basal). Movable finger (Fig. 2) with four teeth: distal internal tooth large, distinctly separated from others; distal external, medial, and basal teeth situated close together at midfinger; medial tooth smaller than either distal external or basal teeth. Distinct serrula present on ventrodiscal two-thirds of movable finger. Dense array of long, thin setae present on medial and ventral surfaces of fixed finger; a few longer hairlike setae situated on ventral aspect of movable finger (proximal to serrula).

Pedipalps: Femur (Fig. 5) with faint dorsoexternal carina present only on basal one-third; other carinae obsolete. All surfaces moderately granular. Orthobothriotaxia C (Vachon 1974). Tibia (Figs. 6-8): carinae essentially obsolete, surfaces uniformly moderately granular. Orthobothriotaxia C (Vachon 1974); trichobothria *db* and *dt* petite; trichobothrium *v*₂ located on external aspect (Fig. 7). Chela (Figs. 9-13): manus slightly swollen, with palm length/chela width ratio of 1.71-1.73; carinae essentially obsolete, but dorsal margin well supplied with coarser granules. All other surfaces moderately to densely granular. Fixed finger (Fig. 12) granular basally, with four slightly oblique rows of denticles limited to distal two-thirds of inner margin; basal row shortest; only three inner accessory granules paired with terminal denticle and enlarged granules of the two apical

rows. Movable finger (Fig. 13) granular basally, with five slightly oblique rows of denticles limited to distal two-thirds of inner margin; basal row short, about as long as apical row; four inner accessory granules paired with the terminal denticle and enlarged granules of two apicalmost rows. Movable finger as long as palm, but distinctly shorter than carapace or metasoma V; fixed finger length/carapace length ratio of 0.60. Orthobothriotaxia C (Vachon 1974); trichobothria *ib* and *it* situated just basal to junction of fixed finger and manus (Figs. 11-12); trichobothria *Db*, *Esb*, *Et₄*, *Et₅*, and *esb* petite (Fig. 10).

Legs: All segments moderately setose. No tibial spurs; only a single pedal spur located on prolateral aspect in arthrodial membrane between tarsomeres I and II (Fig. 14). Ventral aspect of tarsomere II (Fig. 14) with three to four pairs of setae flanking a median row of tiny spinules. Unguis moderately developed, weakly curved; dactyl (median claw) moderate.

Variation.—There was no significant variation in the two male specimens. The subadult female was much paler in coloration, being more or less uniformly cream-colored. This specimen also retains vestigial rows of granules extending to near the base of the pedipalp chela fixed and movable fingers; therefore, it has five rows on the fixed finger and six rows on the movable finger. There are no enlarged basal granules or inner accessory granules on the fourth row on the fixed finger or on the fifth row of the movable finger. This information may indicate that reduction of the number of rows of granules as found in the adults occurs at the maturation molt. In addition, the cuticular surfaces were consistently less granular than in the males. The female also had a malformed right pectine with the two proximal pectinal teeth fused at the base.

Comparisons.—*Typhlochactas mitchelli* differs from the other species of *Typhlochactas* by having only four rows of denticles on the chela fixed finger and only five on the movable finger. Further, these rows of denticles do not extend the full length of the fingers as in the other species.

Typhlochactas mitchelli is most similar to *T. sylvestris* Mitchell and Peck, also from montane forest litter in Oaxaca, México. Both of these species have only three individual teeth on the cheliceral fixed finger, a hypothesized synapomorphy (there are four teeth on the fixed finger in other *Typhlochactas*). There are three external teeth on the cheliceral movable finger in *T. mitchelli* and three or four in *T. sylvestris* (resulting from asymmetry in the holotype). However, the configuration of the teeth is quite different in the two species; the distal tooth in *T. sylvestris* is quite large compared to the others and more closely associated with the distal external tooth, rather than with the other external teeth as in *T. mitchelli* (Fig. 2).

Typhlochactas mitchelli also differs from *T. sylvestris* in the more highly developed granulation of its tergites, metasoma, and pedipalps. The ventral aspect of tarsomere II bears a median spinule row in *T. mitchelli*, but not in *T. sylvestris*. There are also distinct differences in morphometrics: in *T. mitchelli*, (1) the metasoma is proportionately longer, with the sum of metasomal I-V lengths/carapace length 3.04-3.09 (not 2.51) and metasoma V length/carapace length 1.09-1.10 (not 0.99); (2) chela fixed finger length/carapace length is 0.60 (not 0.72); and (3) chela palm length/chela width is 1.71-1.73 (not 1.48).

Comments: *Typhlochactas mitchelli* and *T. sylvestris* are certainly the two smallest described scorpion species in the world. The total length of *T. mitchelli* ranges from 8.49-8.99 mm; that of the holotype (and only known specimen) of *T.*

sylvestris is reported to be 11.05 mm. However, examination of Mitchell and Peck's (1977) table of measurements indicates a disproportionately large mesosomal length measurement, and it is apparent that the authors must have taken a single measurement of the mesosoma (rather than taking the sum of the lengths of the individual segments, as was done here). The intersegmental membranes stretch during preservation, and the degree of stretching will vary with the specimen. Without remeasuring the individual mesosomal tergites of *T. sylvestris*, it is difficult to say which of the two species is actually smaller; the carapace of *T. mitchelli* is shorter, but its metasoma and telson are larger. However, taking a single mesosomal measurement of the two adults of *T. mitchelli* results in total lengths of 9.46 and 9.90 mm, so *T. mitchelli* might be the smaller of the two and, therefore, the smallest known scorpion.

Francke's (1981) cladogram depicting the phylogeny of the Superstitioninae is not greatly modified by the addition of *T. mitchelli*. *Typhlochactas mitchelli* is added at the terminal branch as the sister species of *T. sylvestris*; the synapomorphy justifying their relationship is the joint possession of three teeth on the cheliceral fixed finger. Reduction of the number of granular rows on the chela fingers and the unique configuration of the dorsal teeth of the cheliceral movable finger are autapomorphic characters for *T. mitchelli*.

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**MITES PARASITIC ON SPIDERS, WITH A
DESCRIPTION OF A NEW SPECIES OF
EUTROMBIDIUM (ACARI, EUTROMBIDIIDAE)**

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ABSTRACT

A new species of *Eutrombidium* is described from larvae parasitizing 38 *Ceraticelus emertoni* (O. Pickard-Cambridge) (Araneae, Linyphiidae) and one *Oxyopes salticus* Hentz (Araneae, Oxyopidae) collected in Mississippi. Most host individuals (89%) were parasitized by only one larva, but as many as nine larvae were attached to one host. Adult and immature hosts of both sexes were parasitized. All larval mites were attached to the lateral molt sutures, mostly on the posterior prosoma. A review of the literature reveals 30 records of mite ectoparasitism of spiders among eight mite genera from five continents. Six additional records are reported herein. Two species listed as spider parasites, *Allothrombium metae* Boshell & Kerr (Acari, Trombidiidae) and *Copriphus bristowi* Finnegan (Acari, Laelapidae), are transferred to *Clinotrombium* and *Ljunghia*, respectively.

INTRODUCTION

Larvae of the cosmopolitan genus *Eutrombidium* Verdun (Acari, Eutrombidiidae) parasitize a variety of Orthoptera (Welbourn 1983), whereas the active postlarval instars of at least one species, *E. locustarum* (Walsh), are predators of orthopteran eggs (Severin 1944). Of the 17 nominate species listed by Thor and Willmann (1947), 14 were known from only the postlarval instars. Since then, three additional species have been described from orthopterans. Numerous species remain to be described worldwide.

There are currently three available names for species of *Eutrombidium* in North America: *E. locustarum*, *E. magnum* (Ewing), and *E. corticis* (Ewing). Examination of the type of *Otonia trombidioides* Banks indicates this species should be placed in *Eutrombidium*, *E. trombidioides* (Banks), new combination. *Eutrombidium corticis* should be placed in the Trombidiidae, possibly in the genus *Allothrombium* (Berlese). Two of the remaining three species, *E. magnum* and *E. trombidioides*, are known only from postlarval instars and need to be redescribed on the basis of reared larvae to determine their relationships with the

other named species. All North American larvae reported in the literature have been (mis-) identified as either *E. trigonum* (Hermann) or *E. locustarum*. *Eutrombidium trigonum* is an European species and its presence in North America has not been verified. *Eutrombidium locustarum* larvae have been reported from North American orthopterans representing more than 35 genera in four families (Welbourn 1983; Rees 1973; Huggans and Blickenstaff 1966).

Examination of spiders collected in west central Mississippi revealed larvae of an undescribed species of *Eutrombidium* attached to two different spider species. The absence of previous reports of this mite genus parasitizing spiders and the inadequacy of larval characters used in earlier descriptions justifies our new generic diagnosis and description of the new species. A summary of the biology of this species and a survey and discussion of the general phenomenon of mite parasitism of spiders is also presented.

TAXONOMY

All measurements are in micrometers (μm) unless otherwise noted. Terminology generally follows Welbourn and Young (1987) and Robaux (1974).

Genus *Eutrombidium* Verdun

Eutrombidium Verdun 1909. Soc. Biol. 67:244; Type species: *Trombidium trigonum* Hermann 1804.

Diagnosis.—Larva: Coxal field I with seta *la* nude; coxal fields I, II and III each with thickened and bifid seta, 1b, 2b and 3b respectively; $\text{fnTr} = 1-1-1$; $\text{fnFe} = 6-5-4$; $\text{fnGe} = 4-2-2$; $\text{fnTi} = 6-5-5$; $\text{fsol} = \text{I} (0-2-2-1), \text{II} (0-1-2-1), \text{III} (0-1-0-0)$; $\text{fzeta} = 2-1-0$ or $2-0-0$; famulus on tarsus leg I distal to *omega*; palpal femur and genu each with a minute dorsal or lateral seta; one of three setae (in addition to palpal tibial claw) on palpal tibia spinelike or hypertrophied; palpal tibial claw bifurcate; *sc1* hypertrophied. Deutonymph and Adult: Dorsal idiosomal setae setiform; posterior idiosoma with pygosomal plate; palpal tibia with two rows of dorsal spines and one to four large ventral spines.

Eutrombidium lockleii, new species

Type data.—Holotype (AL-3280) and 55 paratypes ex *Ceraticelus emertoni* (O. Pickard-Cambridge) (Araneae, Linyphiidae) from Mississippi, Sunflower Co., 8 km SSW Indianola, in field dominated by coastal bermuda grass, collected by D-Vac suction method, 19 July 1984, T. C. Lockley. Two additional paratypes from same locality and date ex *Oxyopes salticus* Hentz (Araneae, Oxyopidae). The holotype and four paratypes will be deposited in the United States National Museum, two paratypes each will be sent to the following institutions: Field Museum of Natural History, Chicago; Canadian National Collection, Ottawa; British Museum (Natural History), London; Muséum National d'Histoire Naturelle, Paris; South Australian Museum, Adelaide; University of Michigan Museum of Zoology, Ann Arbor. The remaining paratypes will reside in the Acarology Laboratory, The Ohio State University, Columbus.

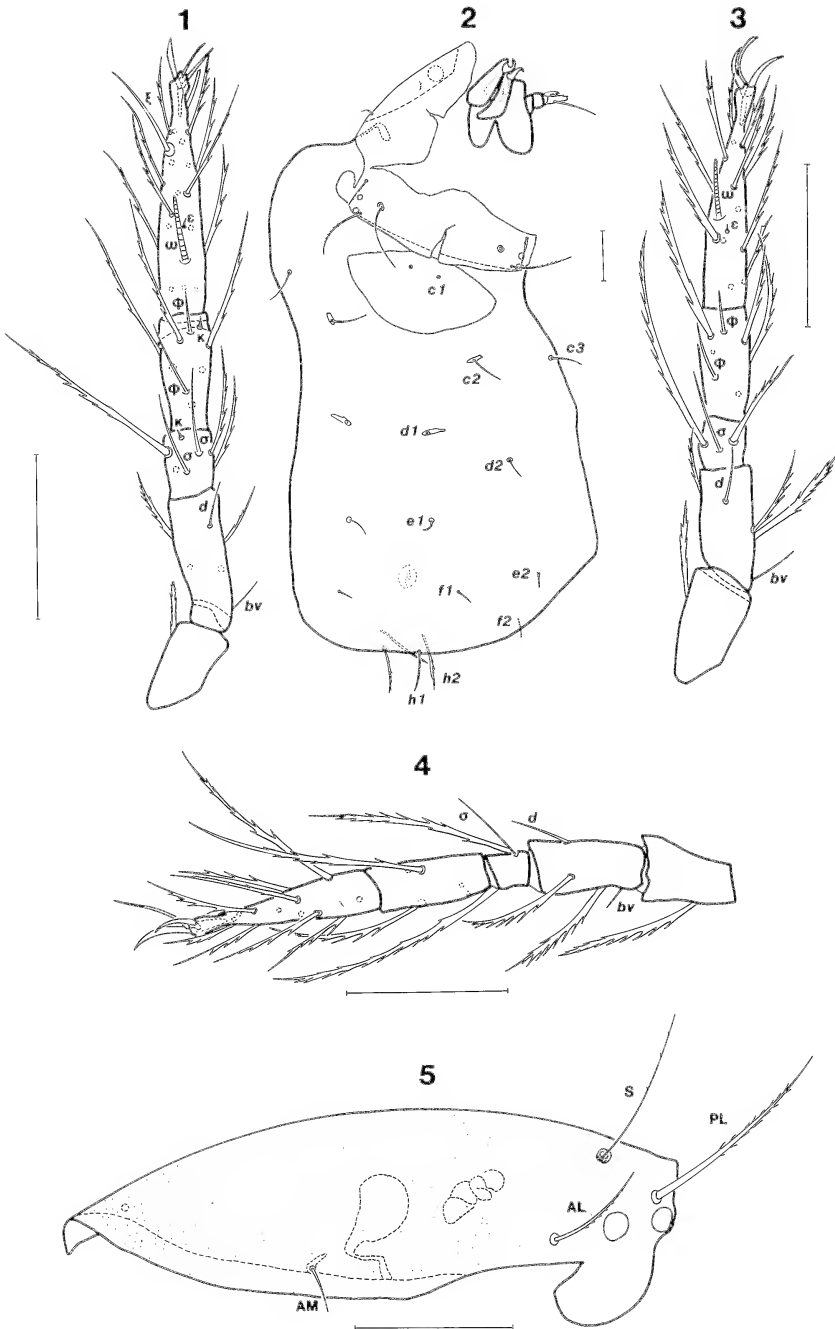
Diagnosis.—Larva with eyes and ocular sclerites incorporated into prodorsal sclerite; genu, legs I, II and III, each with at least one very long barbed seta; palpal tibial claw bifurcate distally and with basal knob; palpal tarsus with one very long barbed seta; lophotrix and scopa on tarsus leg III undeveloped; tarsus leg II without subterminal eupathid.

Description.—Larva: *Idiosoma* (Figs. 2, 6). Holotype partially engorged. Due to distortion during mounting no size measurements were made; unmounted specimens ranged from 200 (unengorged) to 700 (engorged); eyes 2/2 incorporated into prodorsal sclerite, anterior eye smaller. Prodorsal sclerite and scutellum occupy most of the dorsal idiosoma in unengorged specimens, displacing dorsal idiosomal setae posteriorly and ventrally. Setal rows C and D each with three pairs of setae, rows E and F each with two pairs of setae; H and PS rows each with one pair of setae. Setae *c1* on scutellum; *c2* and *d1* each set on narrow sclerites. Idiosomal setae (Figs. 1, 3) *c1* (59-71), *d1* (50-63) longer than setae in rows E (13-29), F (13-20), and setae *c2* (33-39), *c3* (29-38), *d2* (19-22), *d3* (18-23); H and PS setae long, 38-51 and 56-67, respectively. Cupules and supracoxal seta (*e1*) absent. One pair of closely associated, branched intercoxal setae between coxae III; two pairs of preanal setae.

Prodorsal Sclerite (Figs. 2, 5, 6): Punctate without striae, anterior margin convex, posterior margin slightly concave; $PL > S > AL > AM$; $SB < PW$; trichobothridial bases anterior to PL setal bases; trichobothria flagellate, with setules. Scutal measurements of holotype with mean, range and number of paratypes measured given within parentheses: AM 14 (14, 11-17, 19), AA - (61, 58-64, 10), AW - (85, 72-93, 5), AL 33 (33, 28-36, 21), PL 70 (68, 63-72, 22), AP 35 (37, 35-41, 28), SB 139 (131, 123-138, 9), S 72 (65, 56-72, 21), PSB 31 (28, 21-36, 12), ASB - (116, 111-119, 2), SD - (138, 132-145, 2), PW (excluding ocular sclerites) - (186, 172-193, 7). Scutellum: HS 85 (82, 75-90, 26), LSS 175 (166, 157-175, 21), *c1* - (65, 59-71, 14), SS 33 (35, 30-40, 28). Because of distortion of prodorsal sclerite, PS measurement was not made.

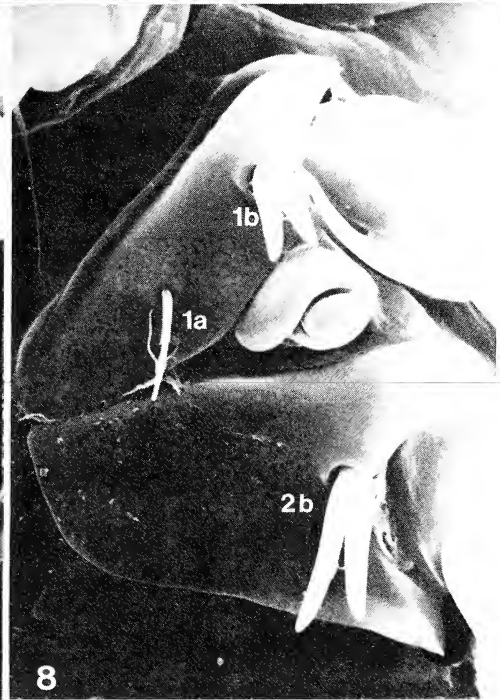
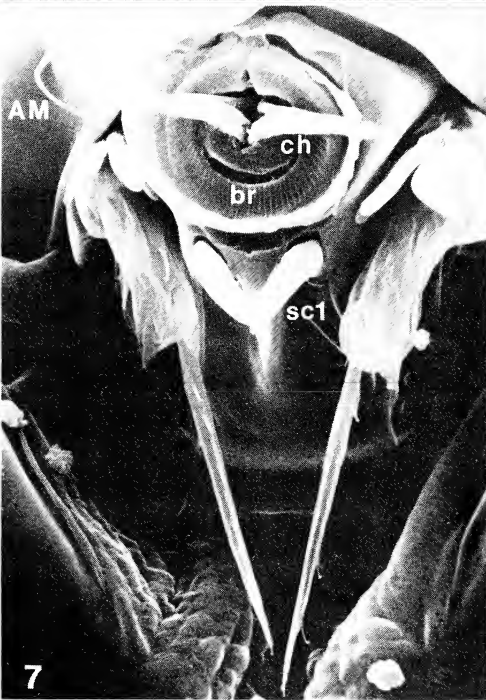
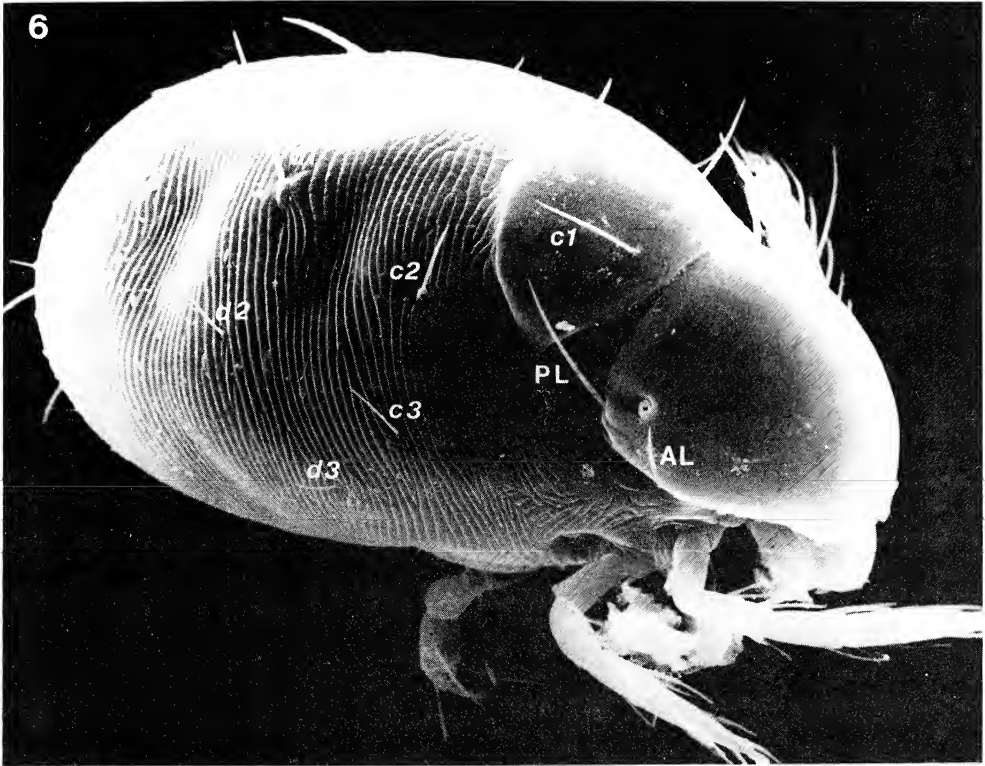
Gnathosoma (Fig. 7): Palpal setal formula N-N-NNS2-7NB *omega* (palpal trochanter absent); palpal tibial claw with two distal prongs and basal knob; adoral setae (*or1*) nude, subcapitular setae (*sc1*) hypertrophied; palpal supracoxal setae (*e*) absent; cheliceral blade (*ch*) with single ventral tooth, surrounded by buccal ring (*br*).

Legs (Figs. 1, 3, 4): Femora undivided, six segments beyond the coxal field; pretarsus legs I and II with paired claws and clawlike empodium; pretarsus leg III with normally developed antiaxial claw and claw-like empodium, but with paraxial claw twice as long as antiaxial claw. Measurements of holotype with positions of specialized setae given as a ratio of the segment length. Mean, range, and number of paratypes measured given in parentheses. *Leg I* 200 (196, 188-204, 25); coxal field (Fig. 8) with two setae, one nude 27 (30, 26-36, 13) and other thickened and bifid 19 (18, 17-19, 14); trochanter 1B; femur 6B, *bv* and *d* setae nude; genu 4B with one seta much longer than others 63 (70, 62-78, 15), two *sigma* 25 (24, 20-28, 18) and 23 (21, 20-26, 18) at 0.32 (0.35, 0.26-0.47, 25) and 0.57 (0.57, 0.47-0.72, 25), respectively, microseta *k* 2 (2, 1-2, 14) at 0.84 (0.84, 0.78-0.90, 14); tibia 6B, two *phi* 22 (19, 15-24, 20) and 16 (14, 11-17, 20) at 0.32 (0.33, 0.26-0.37, 25) and 0.81 (0.80, 0.77-0.84, 25), respectively, *k* 3 (2, 1-3, 8) at 0.91 (0.87, 0.84-0.89, 8); tarsus 18B, *omega* 22 (20, 17-23, 22) at 0.21 (0.25, 0.19-0.38, 25), famulus 3 (2, 1-3, 22) at 0.43 (0.40, 0.36-0.45, 22), two eupathidia 31



Figs. 1-5.—*Eutrombidium lockleii*, new species: 1, holotype leg I; 2, dorsal view of holotype; 3, holotype leg II; 4, holotype leg III; 5, lateral view of paratype prodorsal sclerite. Scale bar 50 μ m. See text for explanation of symbols.

(30, 25-34, 24) and 13 (14, 11-15, 12) at 0.68 (0.70, 0.68-0.77, 25) and 0.86 (0.87, 0.83-0.91, 22), respectively. *Leg II*. 190 (184, 173-192, 24); coxal field (Fig. 8) with one thick, bifid seta 19 (20, 19-22, 14); trochanter 1B; femur 5B, *bv* and *d* setae nude; genu 2B with one seta very long 68 (68, 62-76, 12), *sigma* 17 (21, 15-27, 17)



Figs. 6-8.—*Eutrombidium lockleii*, new species: 6, Scanning electron microscope (SEM) micrograph of engorged paratype (300x); 7, SEM micrograph of ventral gnathosoma (1250x); 8, SEM micrograph of coxal fields of legs I and II (1250x). See text for explanation of symbols.

at 0.36 (0.36, 0.28-0.48, 25), k 2 (2, 2-3, 13) at 0.80 (0.75, 0.70-0.81, 10); tibia 5B, two *phi* 15 (16, 13-21, 19) and 12 (12, 10-14, 14) at 0.35 (0.34, 0.29-0.39, 25) and 0.78 (0.78, 0.70-0.82, 24), respectively; tarsus 14B, *omega* 18 (18, 17-21, 25) at 0.41 (0.42, 0.39-0.45, 25), famulus 1 (1, 1-2, 6) at 0.35 (0.36, 0.32-0.40, 6), without eupathid. Leg III. 173 (172, 165-192, 23); coxal field with one thick bifid seta 18 (18, 16-20, 13); trochanter 1B; femur 4B, *bv* and *d* setae nude; genu 2B with both setae very long 64-83 (62-79, 56-89, 24), *sigma* 25 (21, 17-27, 18) at 0.38 (0.38, 0.29-0.49, 24); tibia 5B, tarsus 13B, scopa and lophotrix undeveloped.

Etymology.—The specific epithet is from the collector's name, T. C. Lockley.

Taxonomic discussion.—Despite the lack of systematic work on North American *Eutrombidium*, *E. lockleii* can be easily distinguished from other *Eutrombidium* in having the ocular sclerites fused into a prodorsal sclerite, eyes on prodorsal sclerite, long barbed seta on palpal tarsus, undeveloped lophotrix and scopa on tarsus leg III, and by the short, rounded idiosoma. It is difficult to assess the relationships of this species with other members of the genus when only six of the 20 named species are known from the larval instar. Only the discovery of the postlarval instars of this species and rearing of additional *Eutrombidium* species will allow the relationship of this unusual species to be clarified.

SUMMARY OF BIOLOGY

All 58 specimens of *E. lockleii* were obtained from one field 8 km SSW of Indianola, Sunflower Co., Mississippi. This 8 ha hayfield was bordered on the east by a 100 ha fallow pasture, on the north by a 40 ha cotton field, on the west by a deciduous tree-lined wet slough, and on the south by a seasonally dry slough. Coastal bermuda grass predominated, with *Erigeron strigosus* Muhl. ex. Willd. (Compositae) the most abundant flowering plant during the sampling period. This field is the same as Site #2 of Young and Welbourn (1987), where another new species of mite was discovered attached to tarnished plant bugs (Welbourn and Young 1987).

During the period of 12 July to 3 September 1984, 10 vacuum samples were collected weekly at this site, each sample representing 25 row-feet. From these collections, 1530 *Ceraticelus emertoni* were obtained. Thirty-eight individuals of this species possessed attached larvae of *Eutrombidium lockleii* (Fig. 9). These collections also contained 208 *Oxyopes salticus*, of which one individual had two attached larvae of *E. lockleii*. Most specimens of *E. lockleii* were obtained on 19 July 84, when 35 of 365 *C. emertoni* had mites attached (9.6% parasitization rate).

The average body length of *C. emertoni* adults was ca. 1.5 mm, and the average body length of unengorged *E. lockleii* was ca. 0.2 mm, though some engorged specimens that were still attached exceeded 0.7 mm and were as long as the host prosoma. Multiple attachments did occur, as three spiders were obtained with two mites each, one spider with six mites, and one spider with nine mites attached. Adult and penultimate male and female spiders, as well as small and large immatures, were obtained with attached mites. Two-thirds of the hosts, however, were immature spiders.

An analysis of the location of attachment of 56 larval *E. lockleii* on 40 *C. emertoni* indicated that all mites were attached along the lines of exuvial

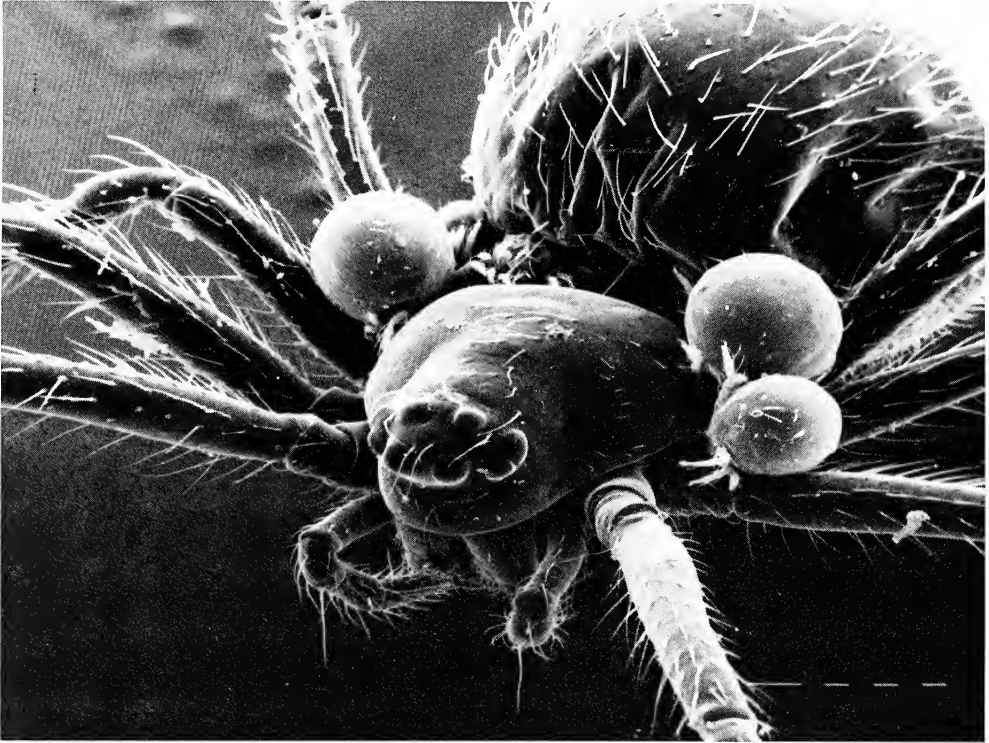


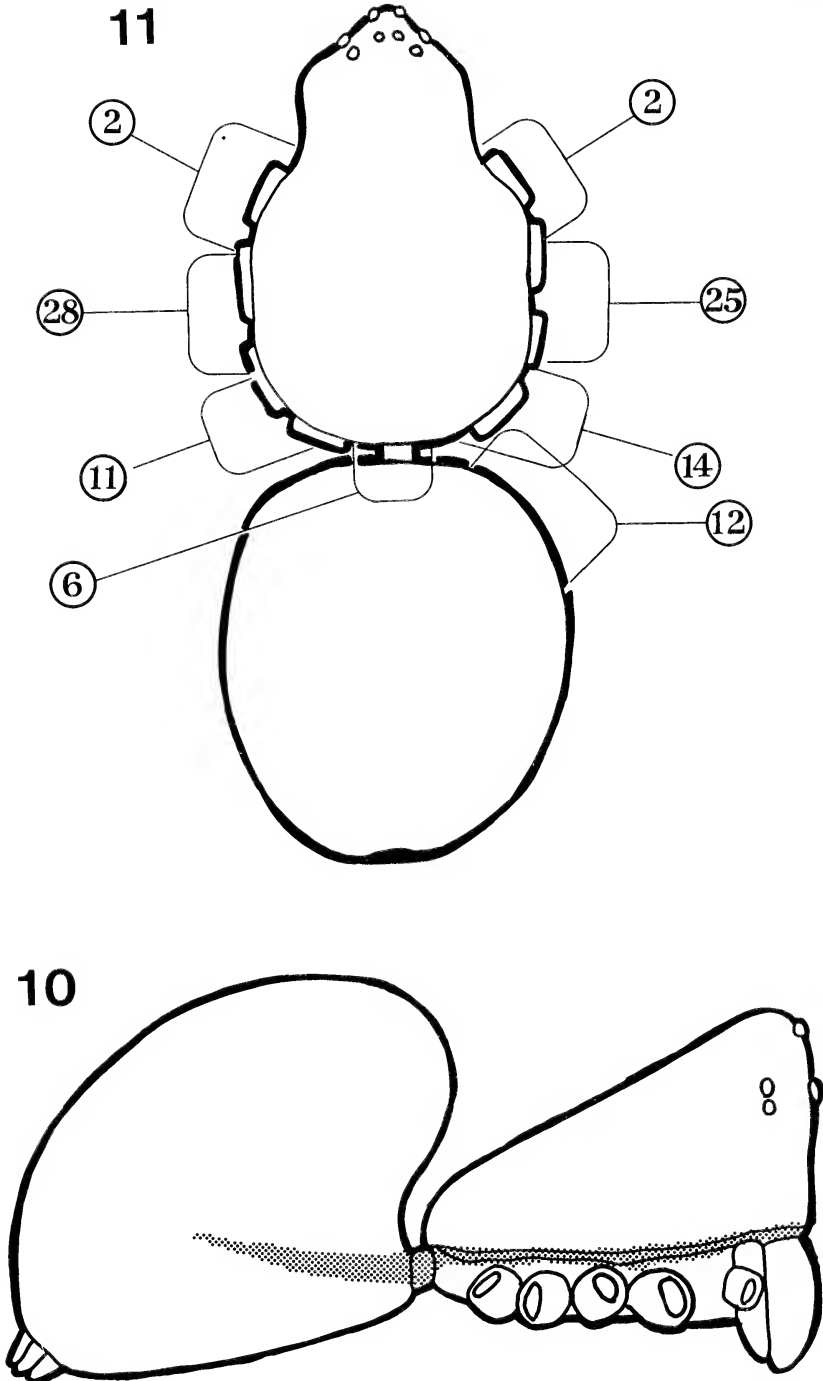
Fig. 9.—SEM micrograph of three larval *Eutrombidium lockleii* new species attached to prosoma of *Ceraticelus emertoni* (550x).

separation (molt sutures) (Fig. 10). This area on each side of the prosoma is also known as the pleuron, a soft and flexible region that allows the stiff carapace and sternum to move in relation to each other (*sic* "pleurae"; Foelix 1982). More than three-fourths of the mites were located in the median and posterior regions of the pleura (Fig. 11). Attachment to the pleura may be due both to relative ease of cheliceral penetration and to enhanced survivability during host molt.

SURVEY OF PARASITIC MITES ON SPIDERS

Spiders have a variety of parasites, with most internal forms in the insect orders Diptera, Hymenoptera, and Neuroptera (Eason et al. 1967). Other internal parasites include nematodes which, while rare, are present in a wide range of spiders (Poinar 1985). Mites, on the other hand, are found on the external surfaces and not all are parasitic. While relatively common on certain species (e.g., Parker and Roberts 1974), few mites are reported from spiders in general, perhaps due to difficulties in mite identification. The most frequently encountered mites are phoretic forms, which are usually deutonymphs of the mite suborder Astigmata and are not considered here.

Parasitic mites on spiders are reported infrequently, with most species protelean parasites of the prostigmatic cohort Parasitengona. Mites of one mesostigmatic genus have been reported as obligate parasites of spiders. Table 1 summarizes 38 records of parasitic mites associated with spiders of at least 18 families.



Figs. 10, 11.—Diagrammatic views of *Ceraticelus emertoni*: Lateral, stippled area is the line of ecdysial separation, attachment area for most larvae of *Eutrombidium lockleii*, new species; dorsal circled numbers represent the percentage of mite attachments to each region.

The Trombidiidae account for 16 of the 32 protelean spider parasites, with 11 records of the Holarctic genus *Trombidium* (Fabricius) on European and North American spiders. Welbourn (1983) reported mites of 10 nominant species from 43 hosts and another 28 hosts with larvae of undetermined *Trombidium* species. Of these 71 host records, only four were spiders, suggesting that they are accidental hosts for these mites. All records of *Trombidium* from spiders involve ground strata forms which are more likely than arboreal forms to come in contact with the unengorged mite larvae.

Mites of two other closely related trombidiid genera have also been associated with spiders. In *Allothrombium*, adults of *A. lerouxi* Moss were reported to attack and kill a *Trochosa pratensis* (Emerton) (= *T. terricola* Thorell) spider in Canada (Moss 1960). The larvae of *Allothrombium* are most often reported from aphid hosts, but there are several records of other arachnid hosts including one from a spider. A second genus, *Clinotrombium* (Southcott), has two of three named species of mites reported as parasites of spiders in Australia (Southcott 1986). Michener (1946) reported *Allothrombium metae* Boshell and Kerr parasitizing *Pirata* spiders in Panama. Examination of Michener's reared specimens indicates that *A. metae* should be transferred to *Clinotrombium*, based on the position of the prodorsal trichobotria and PL setae [= *Clinotrombium metae* (Boshell and Kerr) *new combination*].

The second most reported group of mites parasitic on spiders is the Erythraeidae, accounting for 14 of the 32 records. Nearly half of these records are larvae of the cosmopolitan genus *Leptus* (Latreille). This genus contains approximately 90 named species whose larvae parasitize a wide variety of insect and arachnid hosts. Welbourn (1983) listed 78 arthropod hosts of 30 named *Leptus* species, and an additional 55 hosts of unidentified *Leptus*. From those 133 host records, only three species, *L. hidakai* Kawashima, *L. atticolus* Lawrence and *L. gifuensis* Kawashima, are known from spiders. *Leptus atticolus* and *L. gifuensis* are known only from the type hosts (spiders) in South Africa and Japan, respectively. *Leptus hidakai* was found on a spider as well as on opilionids in Japan (Kawashima 1958). Additional collecting and study is needed to determine if these *Leptus* species are restricted to spiders. The unidentified erythraeid, possibly *Leptus*, on *Diaea* sp. (Thomisidae) from New Zealand was pictured by Forster and Forster (1973) and represents the first record from New Zealand. While most protelean parasites are associated with ground-dwelling spiders, *Leptus* has been found on both aerial and ground-dwelling forms. Two species of *Charletonia* (Oudemans), *C. aranea* Southcott and *C. miyaxakii* (Kawashima), are known only from spiders in India and Japan, respectively, and two new records for the U.S.A. are listed in Table 1. All other species of *Charletonia* are primarily parasites of Orthoptera and other insects. *Lasioerythraeus* Welbourn and Young is a widespread genus in the New World which primarily parasitizes hemipterans, with one record from an immature spider in Mississippi (Young and Welbourn 1987). The new records from Chile (Table 1) represent the southernmost records for the genus.

The mesostigmatic family Laelapidae is a large and diverse group which includes free-living predators, arthropod and vertebrate parasites, and nest associates. Mites of the genus *Ljunghia* (Oudemans) are obligate parasites (non-protelean) of mygalomorph spiders in Indonesia and Australia (Domrow 1975). While all instars can be found on the host, their habits are unknown. This genus

Table 1.—Parasitic mites on spiders.

| Parasite | Host | Country | Reference |
|--|--|-----------------|--------------------------|
| PROSTIGMATA | | | |
| Erythraeidae | | | |
| <i>Charletonia aranea</i> Southcott | Araneae | India | Southcott 1966 |
| <i>C. miyazakii</i> (Kawashima) | <i>Theridion</i> sp. (Theridiidae) | Japan | Kawashima 1958 |
| <i>C.</i> sp. | Araneae | USA(IL) | NEW |
| | <i>Philoponella oweni</i> (Chamberlin) (Uloboridae) | USA(AZ) | NEW |
| <i>Lasioerythraeus johnstoni</i> Welbourn & Young | Linyphiidae | USA(MS) | Young & Welbourn 1987 |
| <i>L.</i> sp. | Cybaeinae (imm.) (Agelenidae) | Chile | NEW |
| | Anyphaenidae (imm.) | Chile | NEW |
| <i>Leptus atticolus</i> Lawrence | <i>Saitis</i> sp. (Salticidae) | South Africa | Lawrence 1940 |
| <i>L. gifuensis</i> Kawashima | <i>Lycosa</i> sp. (Lycosidae) | Japan | Kawashima 1958 |
| <i>L. hidakai</i> Kawashima | <i>Chiracanthium</i> sp. (Clubionidae) | Japan | Kawashima 1958 |
| <i>L. ignotis</i> (Oudemans) | <i>Pachygnatha clercki</i> Sundeval (Araneidae) | England | Parker 1962 |
| <i>L.</i> sp. | <i>Pardosa</i> sp. (Lycosidae) | USA(CT) | Sorkin 1982 |
| | <i>Philodromus imbecillus</i> Keyserling (Philodromidae) | USA(TX) | Cokendolpher et al. 1979 |
| Undetermined genus | <i>Diaea</i> sp. (Thomisidae) | New Zealand | Forster & Forster 1973 |
| Trombidiidae | | | |
| <i>Allothrombium fuliginosum</i> (Hermann) | <i>Lycosa amentata</i> (Clerck) (Lycosidae) | England | Parker 1965 |
| <i>Clinotrombium antares</i> Southcott | Linyphiidae | Australia | Southcott 1986 |
| <i>C. bellator</i> Southcott | Salticidae (imm.) | Australia | Southcott 1986 |
| <i>C. metae</i> (Boshell & Kerr) (New Comb.) | <i>Pirata</i> sp. (Lycosidae) | Panama | Michener 1946 |
| <i>Trombidium poriceps</i> (Oudemans) | <i>Araneus diadematus</i> Clerck (Araneidae) | Switzerland | André 1931 |
| | <i>Dolomedes fimbriatus</i> Clerck (Pisauridae) | Netherlands | Oudemans 1912 |
| | <i>Linyphia</i> sp. (Linyphiidae) | Netherlands | Oudemans 1897 |
| | <i>Nuctenea umbratica</i> (Clerck) (Araneidae) | Switzerland | André 1931 |
| | <i>Zygiella x-notata</i> (Clerck) (Araneidae) | Switzerland | André 1931 |
| <i>T.</i> sp. | Araneae | Canada | Welbourn 1983 |
| | <i>Agelenopsis</i> sp. (imm.) (Agelenidae) | USA(ME) | NEW |
| | <i>Tegenaria domesticus</i> (Clerck) (Agelenidae) | USA(ME) | NEW |
| | <i>Clubiona moestra</i> Banks (Clubionidae) | Canada | Welborun 1983 |
| | <i>Pardosa hortensis</i> (Thorell) (Lycosidae) | Spain | Parker & Roberts 1974 |

| | | | |
|--|--|------------------------|-----------------------|
| | <i>Phrurolithus minimus</i> (Koch) (Clubionidae) | Spain | Parker & Roberts 1974 |
| undetermined genus | <i>Neostothis gigas</i> Vellard (Barychelidae) | Brasil | Vellard 1934 |
| Eutrombidiidae | | | |
| <i>Eutrombidium lockleii</i> , n.sp. | <i>Ceraticelus emertoni</i> (Cambridge) (Linyphiidae) | USA(MS) | NEW |
| | <i>Oxyopes salticus</i> Hentz (Oxyopidae) | USA(MS) | NEW |
| MESOSTIGMATA | | | |
| Laelapidae | | | |
| <i>Ljunghia bristowi</i> (Finnegan) (New Comb.) | <i>Liphistius malayanus</i> Abraham (Liphistiidae) | Malaysia | Finnegan 1933 |
| <i>L. hoggi</i> Domrow | <i>Aganippe subtristis</i> Pick.-Camb. (Idiopidae) | Australia | Domrow 1975 |
| <i>L. pulleini</i> Womersley | <i>Selenocosmia</i> <i>stirlingi</i> Hogg (Theraphosidae) | Australia | Womersley 1956 |
| | <i>Aname</i> sp. (Nemesiidae) | Australia | Domrow 1975 |
| <i>L. rainbowi</i> Domrow | Araneae | Australia | Domrow 1975 |
| <i>L. selenocosmiae</i> Oudemans | <i>Selenocosmia</i> <i>javanensis</i> (Walck.) (Theraphosidae) | Indonesia (Sumatra) | Oudemans 1932 |

was reviewed by Domrow (1975), where he also redescribed *L. selenocosmiae* Oudemans from Indonesia. Another mesostigmatic mite from spiders originally named *Copriphs* (*Pelethiphs*) *bristowi* Finnegan from Malaysia was placed initially in the Eviphididae. Comparison of Finnegan's 1933 description with those of Oudemans (1932) and Domrow (1975) indicates that *C. bristowi* is close to *L. selenocosmiae* and should be transferred to *Ljunghia* [= *Ljunghia bristowi* (Finnegan) *new combination*].

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RESEARCH NOTES

AN IRREGULAR ORB-LIKE WEB BUILT BY AN ADULT MALE
OF *METEPEIRA* SP. A (ARANEAE, ARANEIDAE)

According to Bristowe (1941), Millot (1949) and Foelix (1982) most males of araneid spiders do not build orb webs after their last molt. However, adult males of *Eriophora fuliginea* build orb webs (Robinson et al. 1971; Robinson and Robinson 1981). Laboratory studies corroborated that most males of *Metepeira* sp. A (name suggested by H. W. Levi, *in lit.*) do not build orb webs (Viera and Costa 1985). The objective of this paper is to report an unusual, irregular web built by an adult male of *Metepeira* sp. A.

In the laboratory, 34 adult males were put into individual glass cages (30 × 30 × 9 cm) with a frame and a water container for 48 h. The temperature averaged $23 \pm 2^{\circ}\text{C}$, and the photoperiod was 12 h light/ 12 h dark. A specimen of *Metepeira* sp. A was deposited in the collection of the Museo Nacional de Historia Natural, Montevideo (number 305a).

Only one male built one web within this structure: the web was planar, with a vertical diameter of 22.5 cm, a horizontal diameter of 13 cm, several incomplete

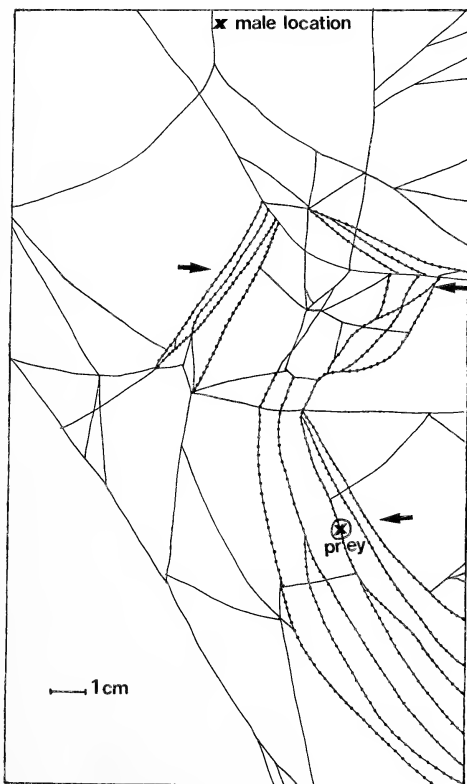


Fig. 1.—Orb-like web of an adult male *Metepeira* sp. A directly drawn from the web. The male built the web in the frame of an experimental cage. Arrows indicate sticky lines. A prey was placed on the sticky lines.

possible radii, and 18 more or less circular sticky lines. Many lines were lax (Fig. 1). One ant (*Acromyrmex* sp.) was placed onto the sticky lines. The prey stuck but the male failed in its capture. However, this male captured another ant in a female web (Viera and Costa 1985) and also mated normally.

This irregular orb-like web resembles webs constructed by young *Zygiella x-notata* (Witt 1956, in Foelix 1982:141) and drugged adult females of *Araneus diadematus* (Witt 1971). Both drugs and sexual maturity in males modify the expression of the innate program of orb web building.

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NORTHERN RECORDS OF *MICROBISIUM BRUNNEUM* (PSEUDOSCORPIONIDA, NEOBISIIDAE) FROM EASTERN CANADA

The range of pseudoscorpion species in Canada is poorly known (e.g., Hoff 1958; Dondale 1979; Sharkey 1987). When collecting invertebrates with pitfall traps and by sieving *Sphagnum* moss in bogs in eastern parts of Canada, 1978 and 1985, the senior author captured the pseudoscorpion *Microbisium brunneum* (Hagen) both in the boreal forest zone and in northern forestline, forest tundra, areas.

M. brunneum was found in samples of *Sphagnum* moss at the following sites in eastern Canada:

1. Ontario; Copetown (43°14'N, 80°04'W), Summit Hill muskeg, 11 July-26 September 1978, 2 exx.

2. Quebec; Parc Jacques Cartier, bog at Lac Barette (47°27'N, 71°15'W), 18 July-14 September 1985, 3 exx.
3. Quebec; Schefferville (54°50'N, 66°50'W), swamp, 21 July 1978, 1 ex.
4. Quebec; Schefferville, open *Sphagnum* bog, 22 July 1978, 1 ex.
5. Quebec; Kuujjuarapik (Poste-de-la-Baleine) (55°15'N, 77°50'W), swamp, 9 July - 29 August 1985, 1 ex.
6. Quebec; Kuujjuarapik, palsa bog, 5-28 August 1985, 1 ex.

It is worth mentioning that *M. brunneum* is the only pseudoscorpion species found at the bogs studied and mentioned above. The habitat fits with the previous data about the ecology of the species: occurring on bogs (Hoff 1946; Sharkey 1987).

According to Hoff (1946), *M. brunneum* has a wide geographical range in eastern Canada and the northern United States. However, no records from eastern Canada (Ontario, Quebec or the Maritime provinces) were included in the list of North American pseudoscorpions by Hoff (1958). Three records have been published for *M. brunneum* in eastern Canada. Nelson (1984) mentioned the presence of the species in Ontario and Quebec, and Sharkey (1987) in Cape Breton Highlands National Park, Nova Scotia. Kaisila (1964) wrote in his paper on pseudoscorpions collected from Newfoundland in 1949: "*Microbisium* sp. (spp.?). These, 11 samples in all, constituted the bulk of the material. Finds were made in all parts of the island". This material, sent to J. C. Chamberlin (Kaisila 1964), probably included *M. brunneum*. In addition, Hoff (1958) listed *M. brunneum* just at the forestline area in Churchill, northern Manitoba (about 59°N), based on the report by McClure (1943) as "near *M. brunneum*".

Besides those specimens collected by the senior author the most northern *M. brunneum* in the Canadian National Collection was taken 40 miles west of St. John's, Newfoundland ex muskeg at about 47°50'N. The present samples of *M. brunneum* from Schefferville and Kuujjuarapik are clearly the northernmost known in the eastern part of Canada. Although the latitude of these sites is more southern than that of Churchill, the environmental conditions are comparable: all these three areas are situated in the forestline region or forest tundra (see e.g., Danks 1981).

M. brunneum is not the pseudoscorpion with the most northern distribution in North America. An undescribed species of *Wyochernes* (presently being described by W. B. Muchmore) was discovered by V. Behan-Pelletier in the Yukon Territory at the following locality: British Mountains, 350 m, Sheep Creek, 69°10'N, 140°18'W, 23 June 1984, collected under stones on fine gravel about 1 m from edge of creek.

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PREDATION OF *ACHAEARANEA TEPIDARIORUM* (ARANEAE, THERIDIIDAE) UPON *SPHODROS FITCHI* (ARANEAE, ATYPIDAE)

Sphodros fitchi Gertsch and Platnick is a recently described purseweb spider inhabiting the central plains states from Nebraska to Oklahoma and Arkansas (Gertsch and Platnick 1980). Although some aspects of the natural history of members of this genus have been observed (Coyle and Shear 1981; McCook 1888; Morrow 1985; Teeter 1984), little information exists concerning predation. A female *Sphodros rufipes* (Latreille) was taken from the stomach of a frog (Gertsch 1936). Observations in eastern Kansas indicate that males of the same species often fall victim to female conspecifics and females of *Sphodros niger* (Hentz) during the mating season (Morrow 1985). The present note records predation of *Achaeearanea tepidariorum* (C. L. Koch) upon *S. fitchi*.

On 10 July 1987, remains of an adult male *S. fitchi* were discovered in the web of a female house spider, *A. tepidariorum*, located in a metal storage building on the University of Kansas Rockefeller Experimental Tract in Jefferson County, Kansas. The web was situated below a wooden shelf against a wall, and was approximately 0.5 m above the concrete floor. The *Sphodros* was wrapped in silk and suspended in the lower portion of the web.

A. tepidariorum is well known for its ability to overpower and consume relatively large prey, including vertebrates (Gertsch 1979). Due to the shriveled condition of the abdomen, the total length of the victimized *Sphodros* was not measured; however, the length of the carapace was 4.1 mm. Since the male holotype of this species has a carapace length of 4.2 mm and a total length of 12.7 mm (Gertsch and Platnick 1980), the estimated length of the prey item is less than 13 mm. The total length of the female *Achaeearanea* was 7.4 mm.

Upon reaching maturity, *Sphodros* males emerge from their burrows and wander in search of suitable mates (Coyle and Shear 1981). During this period, they are especially vulnerable to predation. Fitch (1963) observed a jumping spider, *Phidippus audax* (Hentz) (Salticidae), attack and quickly kill a male *S. fitchi* that was confined in an open glass jar in his laboratory. In view of an interesting account of a trapdoor spider (*Ummidia* sp.) (Ctenizidae) caught by a *Steatoda triangulosa* (Walckenaer) (Horner and Russell 1986), *S. triangulosa* and other theridiids could conceivably prey upon male *Sphodros*.

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COMMENTS ON A WOLF SPIDER FEEDING ON A GREEN ANOLE LIZARD

Reports of terrestrial, araneomorph spiders feeding on vertebrates are infrequent. Cokendolpher (1977. J. Arachnol., 5:184) observed a female *Argiope aurantia* Lucas eating a *Eumeces laticeps* Schneider (broad-headed skink). The present note is the first report of a wolf spider feeding on a green anole.

On 19 February 1988 at 0700 hours, I observed a male *Lycosa ammophila* Wallace feeding on an *Anolis carolinensis carolinensis* Voight (family Iguanidae). The predation occurred in a sandhill community at Wekiwa Springs State Park, Wekiwa Springs, Orange County, Florida. Dominant trees in the sandhill community are longleaf pine, *Pinus palustris* Mill., and Turkey oak, *Quercus laevis* Walt. The understory is dominated by wiregrass, *Aristida stricata* Michx., and saw palmetto, *Serenoa repens* (Bartr.) Small.

A. carolinensis carolinensis is an abundant lizard in this region of the south, found on trees, shrubs, vines, or the ground. The attack on the anole was not observed. The spider may have encountered the anole at night while it was asleep.

I found the spider and anole after opening the back of a Sherman small mammal trap. It is not known if the spider cornered the lizard in the trap or dragged the lizard into the trap after catching it. The anole measured 3.9 cm (snout-vent length) and was found in the chelicerae of the spider.

The anole received two bites which penetrated the body. The first was immediately behind the hind limbs and the second bite was immediately behind the right fore limb. The wolf spider's jaws were located in the second bite area when first observed. The spider dropped the anole, dropped off the door of the trap and disappeared in the litter. A search of the litter failed to produce the spider.

Identification of the spider is based on (1) size, (2) coloration, and (3) the fact the site has been sampled for 18 months with *L. ammophila* being the only large wolf spider of that size and coloration collected. *Lycosa ammophila* is a large spider belonging to the *lenta* group (Wallace, 1942. American Mus. Nov. No. 1185:1-21). It appears that *L. ammophila* is large enough to handle a medium sized anole without any harm coming to itself.

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NOTES SUR LE DEVELOPPEMENT POSTEMBRYONNAIRE DE *TITYUS STRANDI* (SCORPIONES, BUTHIDAE)

Parmi les Scorpions collectés dans la région de Tukurui, Etat de Pará, Brésil (Lourenço, W. R., sous-presse, Bol. Mus. par. E. Goeldi), quelques exemplaires ont été prélevés vivants parmi lesquels une femelle de *Tityus strandi* Werner, 1939, qui s'est reproduite au Laboratoire à Paris, donnant naissance à 3 portées successives, sans nouvelle fécondation, phénomène déjà observé chez des espèces du genre *Tityus* telles *T. bahiensis* (Matthiesen, F. A., 1970, Bull. Mus. natn. Hist. nat., Paris, 2e sér., 41(6): 1367-1370) et *T. fasciolatus* (Lourenço, W. R., 1979, Rev. nordest. Biol., 2(1/2):49-96).

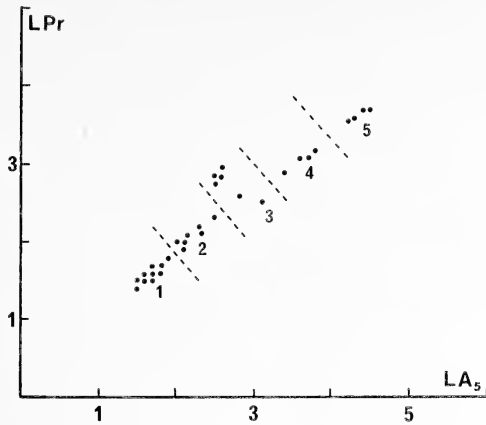


Fig. 1—Distribution des valeurs morphométriques (en mm), pour les stades juvéniles et adulte chez *Tityus strandi*. LPr = longueur du prosoma; LA₅ = longueur du cinquième anneau du metasoma. Chaque point représente au moins un individu.

Les connaissances sur la biologie du développement des *Tityus* d'Amazonie sont encore très incomplètes, et nous rapportons ici les quelques observations faites sur le développement de *Tityus strandi* (Fig. 1).

La femelle étudiée a produit des portées les 28 janvier 1985 (13 petits), 5 juillet 1985 (12 petits), et 25 octobre 1985 (11 petits). Les durées du développement embryonnaire sont donc de 158 jours et 86 jours, valeurs voisines de celles observées pour *Tityus fasciolatus*.

Les petits des 3 portées passent la première mue 4 jours après leur naissance. Seuls 4 individus de la première portée et 5 de la deuxième portée, muent une deuxième fois. Les quatre premiers dans la période du 13 au 15 juin 1985 (à 137 jours en moyenne) et les 5 individus de la deuxième portée entre le 2 et le 5 novembre 1985 (soit à 120 jours en moyenne).

Pour la troisième portée, les observations ont été plus complètes. Tous les 11 individus passent la 2ème mue entre le 1er et le 8 janvier 1986 (à 71 jours en moyenne). Six individus passent la 3ème mue entre le 19 mars et le 15 avril 1986 (entre 145 et 172 jours). La quatrième mue est observée pour quatre individus entre le 13 et le 18 mai 1986 (entre 200 et 205 jours). Finalement le stade adulte est acquis avec la 5ème mue pour quatre individus, 3 femelles et 1 male entre le 30 septembre et le 17 novembre 1986. Ainsi, la durée du développement postembryonnaire se situe entre 340 et 388 jours.

La progression de la croissance est exprimée dans le graphique 1, à partir des valeurs relevées sur les individus morts et les exuvies, mâles et femelles confondus. Sont pris en considération la longueur de la plaque prosomienne (LPr) et la longueur du 5ème anneau metasomal (LA₅). Les résultats obtenus sur le développement de *Tityus strandi* sont voisins de ceux obtenus pour d'autres Buthidae néotropicaux.

Wilson R. Lourenço, Laboratoire de Zoologie (Arthropodes), Muséum National d'Histoire Naturelle, 61, rue de Buffon 75005 Paris, France; and **Vera Regina D. von Eickstedt**, Instituto Butantan, Seção de Artropodos Peçonhentos, 05504, São Paulo, Brasil.

THE JOURNAL OF ARACHNOLOGY

Instructions for Authors

GENERAL COMMENTS

These instructions should be consulted carefully to avoid unnecessary delays in the review, editing, and printing phases of the publication process. **If in doubt, authors should examine the style used in recent issues of *The Journal of Arachnology* and/or consult the Associate Editor.**

Typescripts are preferred in English but are also acceptable in Spanish, French, or Portuguese. They must be **TYPED DOUBLE- OR TRIPLE-SPACED THROUGHOUT**. Good quality paper should be used and erasable bond is specifically excluded. Leave margins at least 1.5 in. (4 cm) on the left and 1 in. (2.5 cm) on the top, bottom, and right. **Do not hyphenate any words at the right margin.** Do not edit your own typescript. *Italics* are permitted only to indicate scientific names; only the TITLE, PRIMARY HEADINGS (e.g., INTRODUCTION, etc.) and RUNNING HEAD should be typed in capital letters. Follow the recommendations of *Council of Biological Editors (CBE) Style Manual*, Third Edition, unless indicated otherwise below. To facilitate prompt review by two or more referees, send to the Associate Editor three identical copies of the typed material, one of which should be designated as the "original", together with photocopies of the illustrations. Original artwork or PMTs may be retained by the author until the completion of the review process and then sent with the revised typescript, or if no revision is necessary, sent at the request of the Associate Editor.

Typescripts longer than about 1500 words (five double-spaced typewritten pages in Elite, six double-spaced typewritten pages in Pica), or the equivalent in printed words plus artwork, should be prepared as Feature Articles, shorter papers as Research Notes. Typescripts and all related correspondence must be sent to the Associate Editor: Dr. Jerome S. Rovner, Department of Zoological Sciences, Ohio University, Irvine Hall, Athens, Ohio 45701 USA.

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Arrange the various parts of feature articles in the following sequence: (1) mailing address, (2) title, (3) by-line, (4) abstract, (5) body of text, (6) acknowledgments, (7) literature cited, (8) figure legends, (9) footnotes, (10) running head, (11) tables with legends, (12) figures. Put only parts 1, 2 and 3 on page 1, and start page 2 with part 4. All other pages are numbered consecutively.

Mailing address.—Include the complete address and telephone number of that author with whom all correspondence with the Editors should be handled.

Title.—When using common or scientific names in the title, be sure to include in parentheses the appropriate higher taxa (order, family,...), but exclude the author of the scientific name. Include footnote indication if appropriate (e.g., to acknowledge grant support), but type footnote separately (see part 9 above). The title should be typed in capital letters and may not exceed 48 characters and spaces per line.

By-line.—Include the name(s) of author(s) as customarily written (less titles) and complete address(es), including zip code or other postal designation. Include footnote indication(s) if appropriate (e.g., to indicate change of address), but type footnote separately (see part 9 above). Leave three spaces between title and by-line, and four spaces between name(s) and address(es).

Abstracts.—The abstract should be a summary of the basic findings, and should not exceed 2 to 3 percent of the text in length. Papers in a language other than English must be accompanied by an English abstract as well as an abstract in the language of the text. Papers written in English but focusing on a subject pertaining to a country where another of the accepted languages is used, may include an abstract in that language.

Body of text.—Use whatever form seems best to accommodate the necessary description of research. Be concise.

Numerals: Use the metric system for all measurements (the English system is acceptable only when transcribing locality data accompanying museum specimens). Write out numbers from one to nine in words unless: (1) there are decimals, or (2) if there is a series of numbers, some of which are 10 or greater, or (3) if they precede standard units of measurement. Time of day should be indicated using the 4-digit, 24-hour clock style without punctuation and with "hours" spelled out. Use the period rather than the comma as a decimal point.

Abbreviations: Conform to standard references for abbreviations, i.e., the *CBE Style Manual* for scientific abbreviations, and a good language reference. Note that abbreviations of metric units of measurement are not punctuated (e.g., mm and km, but ft. and mi.). Some common abbreviations should be typed as follows: h (hours), min (minutes), s (seconds). Most statistical and arithmetic symbols are italicized: *P* (probability), *N* (sample size), *df* (degrees of freedom), *t*-test; but SD (standard deviation), SE (standard error). Years should be written in full, e.g., 1988-1989, not 1988-89. Write out "male" or "female" rather than use symbols.

Citations: Citations within the text should be in the following form: Bellrose (1950); Bellrose (1950:33); or (Bellrose 1950), unless the citation is for the author of a scientific name, and then use a comma between name and date (Bellrose, 1950). The complete scientific name of a species or genus of arthropod, including author(s), must be given the first time it is mentioned in the text. Use single-line notation for fractions [e.g., 1/4 and not ¼; (4-12)/3 and not $\frac{4-12}{3}$].

Whenever an author indicates an unnamed taxon, (e.g., *A-us* sp. or *A-us* sp. A), there must be a designated voucher specimen deposited in a recognized institution and a statement indicating the location of this specimen. It is also recommended that voucher specimens be designated for taxa whose identity may be difficult or uncertain.

Taxonomic papers: The following special directions apply to authors of taxonomic papers:

(a). Do not use abbreviations in a primary heading to indicate that a new name or a new combination is being proposed (e.g., *A-us-x-us*, **new species**, rather than *A-us x-us*, **n. sp.** or comparable abbreviations).

(b). Keys must be typed as follows:

1. Arabic numerals to designate the leading entry of a couplet2
Do not designate the second entry of a couplet, either by means of numbers, letters or other marks*A-us x-us*
2. Type numbers flush to left margin, and start entry on fifth space*A-us y-us*
Subsequent lines of any entry must also be indented five additional spaces as in this example of an entry with two or more printed lines*A-us z-us*

(c). Synonymies must follow the abbreviated style shown below:

A-us x-us Jones, 1930:3, 1935:9; Russell 1945:453; Smith 1954a:16, 1954b:678; Cooper and Lim 1955:18 (in part).

A-us y-us Bates, 1932:18, fig. 4. NEW SYNONYMY.

A-us z-us: Miranda 1948:98 (misidentification): Harris 1951:3 (in part?). (*nec A-us z-us* Zimmer).

(d). Lists of specimens examined of a given taxon must be the last items typed in the treatment of that taxon as they will be set in smaller type. Adhere to the following style for listing specimens examined: Country: State or comparable political subdivision; County or District, detailed locality (elevation), 14 July 1945 (collector), 2 males, 5 females (acronym of institution where specimens are deposited), next detailed locality within that County, etc.; next County in the same State; etc.: next State in the same Country: etc. Next Country: etc. Punctuation rules are very simple. Use a period to separate countries, a colon to separate states, a semi-colon to separate counties, and a comma to separate specific localities.

Acknowledgments.—Avoid overlooking persons who have in some substantial way assisted with the work. Authors of taxonomic papers should spell out the name and indicate parenthetically the acronym of institutions where specimens studied are deposited, if not mentioned elsewhere in the text.

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Figure legends.—Provide one legend for each illustration which will be reproduced separately, or for each "plate" consisting of several illustrations. Adhere to the following styles:

Figures 1-4.—*A-us x-us*, male from Timbuktu: 1, left leg; 2, right chelicera; 3, dorsal aspect of genitalia; 4, ventral aspect of abdomen.

Figures 27-34.—Right chelicerae of species of *A-us* from Timbuktu: Figs. 27, 29, 31, 33.—Dorsal views; Figs. 28, 30, 32, 34.—Prolateral views of movable finger; 27, 28, *A-us x-us*, holotype male; 29, 30, *A-us w-us*, male; 31, 32, *A-us z-us*, holotype male; 33, 34, *A-us t-us*, male. Scale = 1.0 mm.

Type all figure legends consecutively on the same page(s), double spacing lines within each legend and leaving 4 spaces between legends. Keep in mind that 99 characters and spaces represent one

printed line, and that 4 mm for each printed line must be subtracted from the maximum height permissible on full-page illustrations.

Footnotes.—Footnotes will be permitted on page 1 when it is appropriate to acknowledge grant support and to indicate change of address, etc. No footnotes will be permitted on any other page. Type footnotes together on a separate page.

Running head.—At the top of each right hand page will be printed the author(s)' last name(s) and an abbreviated title. This running head may not exceed 60 characters and spaces, must be typed in capital letters, and a hyphen must separate the name(s) from the title. **Place the running head on a separate page.**

Tables with legends.—Prepare all tables precisely as they are to be typeset and include the legend at the top of each. Only in special cases will tables be photo-reproduced rather than typeset. Construct tables as simply as possible. Make marginal notations in the text which clearly indicate the appropriate point of insertion of each table. Note that in these instructions "graphs" are regarded as "Figures," not "Tables."

The size of the printed page imposes a limit on the size of tables that can be accepted. In a normal, upright table these limits are 99 characters and spaces per line and 56 lines in height, including legend. Sideways tables are difficult to typeset and present problems during paste-up; therefore, they will be accepted in exceptional cases only, as most tables that are "too wide" can usually be rearranged to fit into the more desirable, upright position. Any table that exceeds the dimensions given above may not be accepted for publication. Tables must be typed **double-spaced throughout**, and the legend must be in the following style:

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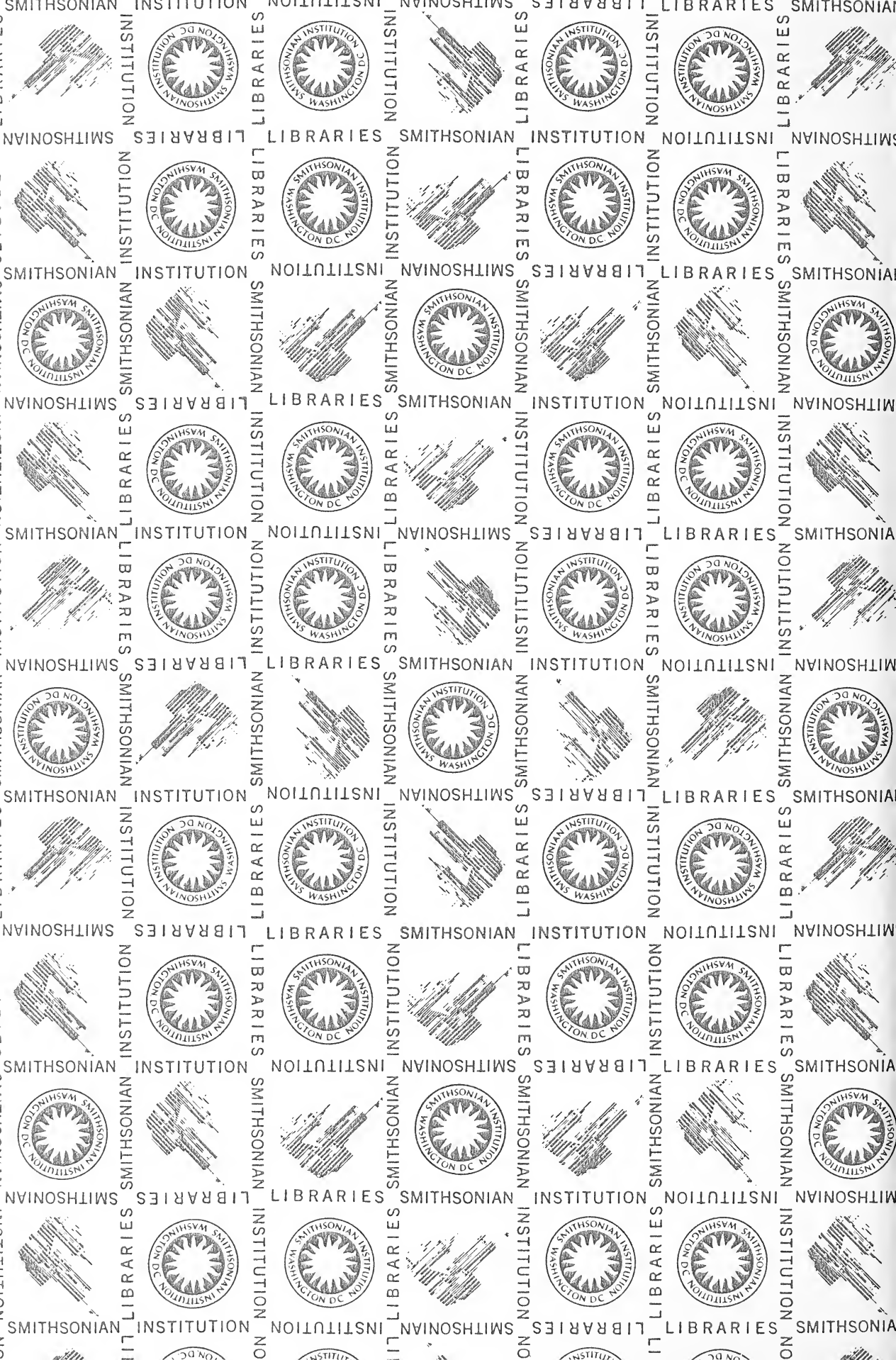
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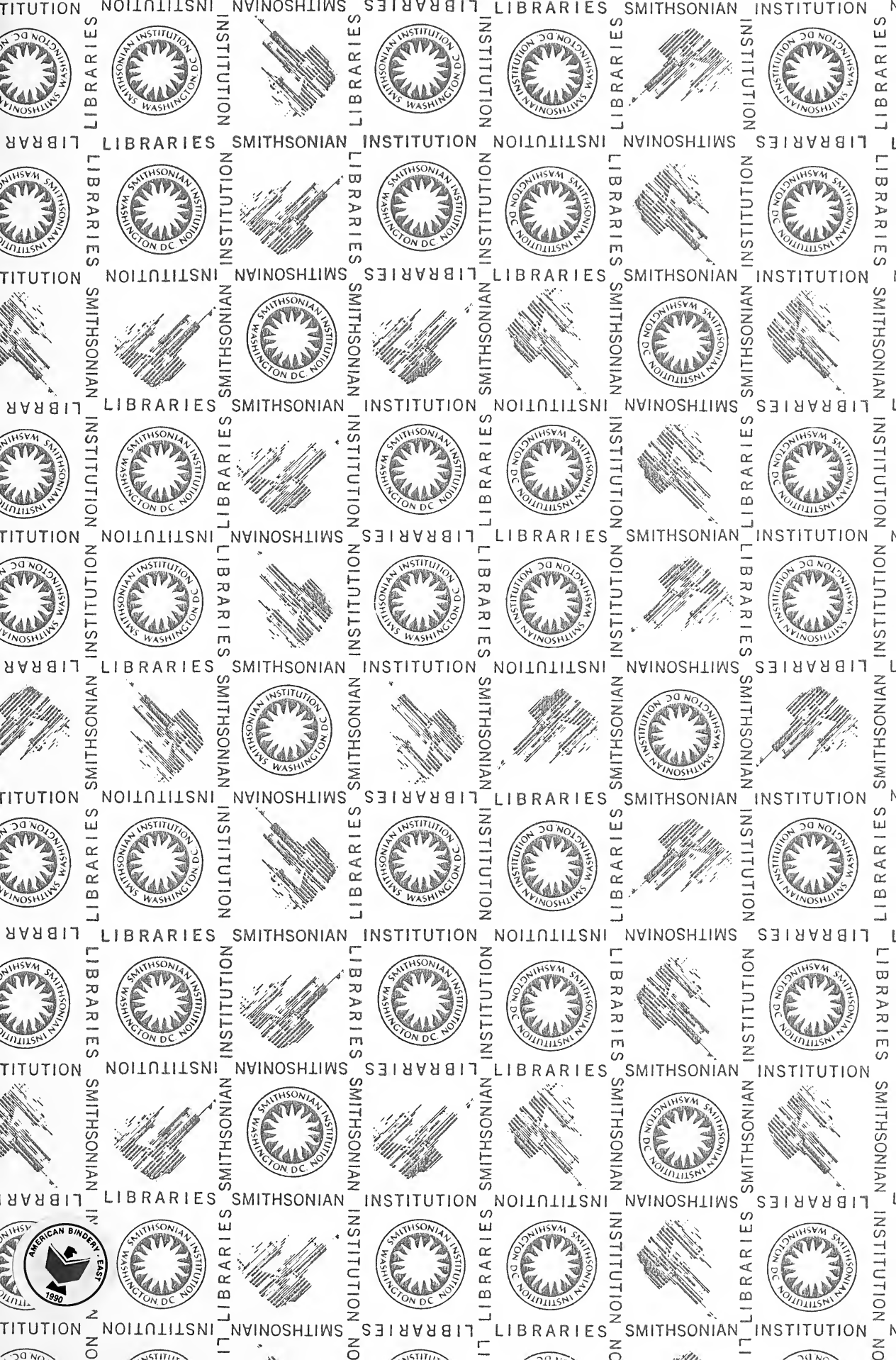
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Cover photograph, spider figure on men's meeting house, Palau, by J. W. Berry

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